ECOLOGICALLY RELEVANT LOW FLOWS FOR RIVERINE BENTHIC MACROINVERTEBRATES: CHARACTERIZATION AND APPLICATION

Rebecca Elizabeth Tharme

Thesis presented for the degree of

DOCTOR OF PHILOSOPHY

In the Department of Zoology

UNIVERSITY OF CAPE TOWN
South Africa

June 2010

ECOLOGICALLY RELEVANT LOW FLOWS FOR RIVERINE BENTHIC MACROINVERTEBRATES: CHARACTERIZATION AND APPLICATION

Rebecca Elizabeth Tharme

Thesis presented for the degree of

DOCTOR OF PHILOSOPHY

In the Department of Zoology

UNIVERSITY OF CAPE TOWN
South Africa

June 2010

For my family

and

For our rivers

A flowing river

You are lovely as a river
under tranquil skies -
There are imperfections
but a music overlays them -

Telling by how dark a bed
the current moves
to what sea that shines
and ripples in my thought

(William Carlos Williams)

ABSTRACT

Ecologically relevant low flows for riverine benthic macroinvertebrates: characterization and application

Rebecca E. Tharme
June 2010

Intensifying hydrologic alteration and the resultant degradation of river ecosystems worldwide have catalyzed a growing body of ecohydrological research into the relationships between flow regime attributes, physical habitat dynamics and biotic response, particularly for determining environmental flows. While invertebrate response to floods has received most attention, in this thesis the aim was to identify and characterize low flows that constituted various degrees of physical disturbance to benthic macroinvertebrate assemblages of perennial rivers.

Experimental reductions in dry-season low flows, of *c.* 36, 85 and 86%, were achieved using temporary diversion weirs, in four perennial upper rivers of the southwestern Cape, South Africa; one river represented a control site. In the context of the characteristic long-term flow disturbance regimes to which reach invertebrate assemblages were adapted, all discharge reductions represented extreme events below the natural minima on record, and for extended durations.

Natural and particularly, manipulated low flows, resulted in consistent marked declines in physical habitat availability for invertebrates, with increased habitat fragmentation, hydraulic biotope isolation, and dominance by low-velocity shallow biotopes. Generalised trends with discharge reduction were identifiable for riffle, run and pool biotopes, as robust, ecologically meaningful patch units that became hydraulically most distinct at lowest flows. Invertebrate responses to low-flow disturbances, in contrast, were often river specific, subtle or inconsistent, requiring multi-scale lines of evidence for their elucidation. The biotope proved the most appropriate geomorphic scale at which to examine the patchy dynamic nature of flow-mediated invertebrate redistribution and refugium use, within the riverscape mosaic. Many invertebrate assemblages and taxa showed distinct, naturally differing biotope specificities and hydraulic tolerances that strongly influenced their characteristic responses to low flows. With the shift from natural to abnormally low flows, considerably fewer invertebrates retained significant biotope affiliations and their relationships with hydraulic factors weakened.

Characterization of ecologically relevant low flows was most effective when indices of invertebrate response were explicitly linked with key monthly and annual flow indices, reflecting differences in site flow histories, coupled with chemical and biotope-scale habitat measures of disturbance. Study results underscored the importance of, and complexities inherent in, deriving generic low flow-invertebrate response models for river management.

Keywords: ecohydrology, perennial rivers, low flows, disturbance, benthic macroinvertebrates, hydraulic biotopes.

ACKNOWLEDGEMENTS

I am so grateful to the numerous colleagues who have become such firm friends, who gave of their time, support and advice during the long path to completion of this thesis. The list is extensive, and some persons have moved on to new destinations:

- Particular thanks to all my friends at the Freshwater Research Unit (FRU), Zoology Department, University of Cape Town: Kate Snaddon, who provided invaluable field assistance during the pilot study; Denise Schael, for advice on graphics and discussions on patch dynamics; and Liz Day, Heather Malan, Helen Dallas, Geordie Ractliffe, Alison Joubert, Bryan Davies and Charlene Coulsen for friendship and ready sources of information.
- Arthur Harrison is warmly thanked for his ever enthusiastic and expert identifications of hundreds of Chironomidae, giving of his precious retirement time to assist with the collection of adult invertebrate material, and for many inspiring discussions on taxonomy and freshwater ecology.
- Sincere thanks must go to: Drew Birkhead (Centre for Water in the Environment, University of the Witwatersrand) for his hydraulic model and guidance on how to use it; Roy Wadeson (Geography Department, Rhodes University) for biotope debates; Bill Rowlston (Head of Hydraulic Studies Subdirectorate, DWAF), Pretoria Albert Rooseboom (Head of Department, Civil Engineering, University of Stellenbosch) and the late André van Niekerk for their sensible advice on flow diversion techniques and hydraulics during the experiment planning stage.
- Many other friends and colleagues involved in the development of environmental flow approaches, from whose experience I benefited greatly: Angela Arthington and Mark Kennard (Griffith University, Australia); Denis Hughes, Tally Palmer and Des Weeks (IWR, Rhodes University); the late Nigel Kemper; Neels Kleynhans (Institute for Water Quality Studies, Department of Water Affairs and Forestry, DWAF); Delana Louw (Environment Studies, DWAF); Malcom Newson and Catherine Padmore (Department of Geography, University of Newcastle, UK); Sharon Pollard (Wits Rural Facility); Kate Rowntree (Geography Department, Rhodes University),
- Jonathan Musikanth, Rachel Spencer and Helen Buckley provided invaluable field assistance during much of the study. Tougheeda Mohamed, our FRU laboratory assistant, is thanked for working tirelessly and with good humour on the lengthy task of sorting samples in the lab. Thanks also to Hugo van Zyl and others who helped out on occasion in the field - it was certainly fun.
- The Surveying Division of DWAF, Worcester, and Dirk van der Boon especially, are thanked for their willingness to be involved in the study and for participating in a field test of survey procedures. Mauritz Acker, Danie Oosterhuizen and their staff are thanked for their efforts and uncharged-for time for the construction and dismantling of the flow diversion structures. Without their expertise such a diversion experiment would not have been possible. The Division is also thanked for free provision of all diversion materials, including a specially constructed scour plate for the temporary diversion of the Molenaars River at the existing gauging weir. DWAF land surveyors Billy West and Reece Hanning helped survey cross-sections, with able field assistance from members of DWAF Worcester: Goodman Gxilishe, Nuna Fena, Wilson Zenzile, Wilson Nelani, James None, Solly Tities and Douglas Buyiselo. Suzaan Nieuwenhuizen and Erick Nieuwenhuizen plotted preliminary survey maps.
- Frans Mouski and other members of DWAF Regional Office, Western Cape, are thanked for permission to alter the hydrological gauging record for the Molenaars River at H1H018 during the flow experiment. They also gave the requisite permission for intensive fieldwork to be conducted in the vicinity of the gauging weirs, and agreed to delay routine scouring of the Molenaars weir pool until such time as the field experiment was completed. The DWAF is also acknowledged for unlimited access to flow gauging sites and weirs during the pilot study.
- Francette Myburgh and Peter Rademyer of DWAF Hydrology Division, Pretoria, provided historical flow records and useful information on weir calibration methods and accuracy, respectively. Other members of DWAF

Hydrology Division are thanked for prioritizing the updating of flow records from the Elands and Molenaars gauging weirs, so that flow records were available for the study period and in time for use in this thesis.

- Mark Gentle of Cape Nature Conservation (CNC) most kindly arranged permits for fieldwork and the collection of samples in the Elands and Molenaars Rivers, and within the Hottentots Holland Nature Reserve. The CNC offered free, unlimited use of their cottage at the Boland Hiking Trail Offices during Riviersonderend River fieldwork. The SAFCOL permitted access to the Riviersonderend site via Grabouw forestry areas. The Chief Forestry Officer is thanked for times when he willingly interrupted work to clear access roads.
- Liz Day, FRU, and Linda Harrower, Chemical Engineering, UCT, ran many water chemistry analyses. The Department of Geology and Geochemistry, UCT, allowed the use of their ICP equipment for cation and anion analyses; James Willis of that Department gave advice on chemical analyses. Access to a TECHNICON AutoAnalyser II was provided by the Seaweed Research Unit (Botany Department, UCT). The FRU is thanked for the loan of its little red bakkie and the Zoology maintenance staff for keeping it clean and roadworthy. I must also thank the UCT library staff, and in particular the interlibrary loan service, who scoured international libraries to find the literature I needed, as well as various UCT administrative and postgraduate offices. Andrea Plos readily helped out with computers. Craig Johnson and Amos Barkai (Institute of Marine Biology, Zoology Department, UCT), guided the experimental design. John Field (Institute of Marine Biology, UCT), permitted the use of laboratory equipment, and advised on the use of Primer. Podge Joska (Botany Department, UCT) provided specialist identification of freshwater algae. Helen James and Ferdy de Moor of the Albany Museum, Grahamstown, and Mike Picker, Zoology Department, UCT, provided much needed literature on invertebrate taxonomy.
- Ninham Shand Consulting Engineers (NSI), Cape Town offered the use of their hydrological programs and provided ready access to reports. André Greyling assisted whenever help was needed, and his support and that of other NSI colleagues is gratefully acknowledged. Advice on hydrological analyses was also given by André Görgens (Department of Civil Engineering, Stellenbosch University). Flow data were patched by Vladimir Smakhtin (IWR, Rhodes University).
- Jacques Hollands (Civil Engineering, University of Stellenbosch) assisted with site selection during the gauging weir survey. Farmers too numerous to mention by name are thanked for access to rivers on private land during that survey. Cape Province transport authorities allowed me to use the Huguenot Tunnel access road for fieldwork on the Elands River.
- David Molden and Frank Rijsberman (International Water Management Institute), and Eloise Kendy and Brian Richter (The Nature Conservancy), need to be thanked for their encouragement during the final stage of this thesis while I was doing my protracted balancing act.
- The South African Water Research Commission (WRC) is acknowledged for funding the two research projects, over the course of which the thinking behind this thesis developed. Project managers Peter Reid and later, Steve Mitchell, had the foresight to encourage and support new directions in applied freshwater research and are thanked most sincerely for their consistent support.
- Sincere thanks must go to Jay O'Keeffe (Institute for Water Research, IWR, Rhodes University), for his positive support and friendship throughout, many fruitful discussions on environmental flows, and some interesting suggestions on invertebrate sampling methods.
- I would like to specially thank Jackie King, my co-supervisor, who so ably led the two WRC projects that provided me with the background training and concepts needed to tackle this thesis, whose dedication to her work was a true inspiration, and who was always first to encourage me to go further.
- I also wish to sincerely thank Jenny Day, the Director of FRU and my supervisor, who still had faith in me at times when I had little left and who was my sounding board so many times in my early career - I thank her for her leadership and clear advice, her infinite patience, which I tested so greatly during the course of this thesis, and her tremendous sense of fairness.
- My final thanks need to go to my family, for wholeheartedly supporting the career I chose, for buying me my first microscope, for always being there for me when I needed them, and for instilling in me the desire to always give of my best and with enthusiasm.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

PAGE

LIST OF FIGURES

PAGE

1. INTRODUCTION

1.1 THE SOUTH AFRICAN CONTEXT AND RESEARCH RATIONALE

1.1.1 Availability and use of water resources

South Africa like much of the rest of southern Africa is predominantly semi-arid, with a Mean Annual Precipitation (MAP) of 452 mm, little more than half the world average of 860 mm (Department of Water Affairs, DWA, 1986; O'Keeffe 1995). Although there are seven different rainfall regions within its borders, tracking an increasing aridity gradient from east to west (Dyer 1976), 65% of the country receives less than 500 mm of rain annually, while 21% is arid (< 200 mm a^{-1}; Davies and Day 1998). Moreover, the conversion of MAP to Mean Annual Runoff (MAR) is only 8.6 %, in contrast with 9.8% for Australia (the most arid continent) and 65.7% for Canada (Alexander 1985; O'Keeffe 1995; Davies *et al.* 1995).

Not only a dryland country, South Africa exhibits marked hydro-climatic stochasticity and correspondingly uneven distribution of freshwater resources, both spatially and temporally (Alexander 1985; DWA 1986; Uys and O'Keeffe 1997a). South African rivers, along with Australian systems, are those with the greatest intra- and inter-annual variation worldwide (Puckridge *et al*. 1998; Poff *et al*. 2006a). The mean coefficient of variation (CV) of MAR for South African rivers is around 117% (> 83 rivers) as compared with 20-53% for many other countries (but excluding an independent estimate for Australia; Van Biljoen and Visser unpubl., cited in Davies *et al.* 1995; Puckridge *et al.* 1998). The country's rivers are prone to greater extremes of flooding and drought than rivers of most countries (Alexander 1985), and some 44% of the rivers by length have a naturally temporary flow regime (Davies *et al.* 1993; O'Keeffe and Uys 1998). Davies *et al.* (1995) identified the combination of high hydrological variability and unpredictability as perhaps the most important difference between 'typical' southern African riverine ecosystems and corresponding systems in North America and Europe.

The country's MAR is 51.1 x 10^9 m^3 a^{-1}, of which only 33 x 10^9 m^3 a^{-1} is practicably usable (O'Keeffe 1995). The need to create reliable sources of freshwater in a water scarce country with the above hydroclimatic constraints, coupled with a transitional economy, rapid population growth and accelerating sectoral water demands, led to the water resources of South Africa being developed and managed in the past with an almost exclusively utilitarian focus (Davies *et al.* 1993). The primary users are irrigated agriculture (*c.* 69%), followed by industry, and municipal and domestic water supply (DWA 1986; Davies and Day 1998). As a result, river regulation, primarily through impoundment, has been prolific, particularly between the 1930s to mid-1970s (Noble and Hemens 1978), to the extent that the major dams in South Africa now have the

capacity to harness more than 52% of total MAR (Davies 1979; DWA 1986; WCD 2000). All of the country's major rivers have been regulated (Davies and Wishart 2000), with South Africa 11th in the top 20 countries worldwide in terms of its number (*c.* 791) of large dams (Chenje and Johnson 1996; WCD 2000). Moreover, the large-scale transfer of water across catchments via inter-basin transfer schemes (IBTs) is considerable (Snaddon and Davies 1999; Snaddon *et al*. 1999). Other smaller-scale off-channel diversions, run-of-river pumped abstractions and impoundments, such as farm dams, have also contributed significantly cumulatively to runoff capture. For example, Adams (1991) recorded over 4000 farm dams with a total storage capacity in excess of 100 million cubic metres (Mcm) in the Western Cape Province alone.

As a result of intensive flow regulation and water abstraction, many of South Africa's naturally perennial rivers have been transformed into temporary systems (or the converse), while others now exhibit unseasonal flow regimes, extremely low flows, or even periodic flow cessation (Davies 1979; O'Keeffe *et al.* 1989a; Davies *et al.* 1995; O'Keeffe 1995; O'Keeffe and Uys 1998). The current degraded ecological condition of many of the country's river systems bears testimony to such intensive hydrological alteration (Allanson *et al.* 1990; Davies *et al.* 1993; Davies and Day 1998; Davies and Wishart 2000).

1.1.2 Policy reform in water resources development and management

Historically, such exploitation of South Africa's surface water resources (and groundwater, though less well documented; Davies *et al*. 1993) was fuelled by the traditional thinking of water users and managers that any water flowing to the sea was wasted (Wadeson 1996; Snaddon and Davies 1998). This mindset persisted despite growing concerns about the deteriorating quality of available freshwaters, and with the longer-term and long-distance costs of ecosystem degradation largely externalised in water resource developments (Davies *et al.* 1993; King and Tharme 1994). During the 1980s, however, a growing awareness emerged within the South African Department of Water Affairs and Forestry (DWAF, formerly DWA) and associated community of water resource managers, of the connection between hydrological alteration and detrimental impacts on rivers, and of the consequent implications for longer-term resource sustainability and human wellbeing (King and Tharme 1994; O'Keeffe 1995; Wadeson and Rowntree 1998). For this and other reasons, including the country's democratization, DWAF initiated a significant and novel shift in policy and legislation from that which supported demand-driven provision of water towards more sustainable, equitable and optimal management of existing water resources (Palmer 1999). Consequently, for the past fifteen or so years, several South African institutions, including DWAF, research funding bodies, academic institutions and conservation authorities have been involved in activities designed to contain or, in some cases reverse, deterioration in the flow-related condition of the country's rivers (King and Tharme 1994; Tharme and King 1998). The water crisis also generated renewed interest in better understanding the ecological functioning and flow-related needs of the region's rivers (Davies *et al*. 1995).

Establishment of the ecological Reserve

The enlightened move by the DWAF to reform water policy paved the way for formal recognition of the natural environment as a legitimate water user with specific needs, and one that required protection as the resource base (Palmer 1999). It also provided the much needed impetus for local ecohydrological research focused on the environmental flow needs of rivers (Tharme and King 1998; Hughes 2001). From then on, in tandem with and capitalising on the growing body of environmental flow knowledge and expertise, considerable advances were made during the 1990s that culminated in the Water Law Principles of 1996, the National Water Policy of 1997, and finally, the new South African National Water Act No. 36 of 1998.

The Act, which sets out the framework for the future management of water resources in South Africa, was acclaimed internationally in that it assigns priority in terms of water allocation to the Reserve, the only water right by law (DWAF 1999a). The Reserve comprises two components, namely the quantity and quality of water required to (1) satisfy basic human needs by securing a basic water supply, and (2) the ecological Reserve for protecting aquatic ecosystems, in order to secure ecologically sustainable development and use of a water resource (Principle C3 of the Act). The Act effectively gave legal status to what had been best practice for close on a decade already - determination of the environmental flow requirements for all rivers proposed for water resource development (O'Keeffe 1995, 2000). It makes provision for the complementary, interdependent strategies of source-based controls (e.g. waste discharge standards) and resource-directed measures (RDM). Within a seven-step generic RDM procedure, most highly developed for rivers, determination of the ecological Reserve (the EFR) is possible at multiple levels of resolution (DWAF 1999a; O'Keeffe 2000; Hughes and Hannart 2003; Section 1.5).

Thus, at the inception of this thesis, a newly established paradigm for integrated water resources management (IWRM; Agarwal *et al*. 2000) was in place in South Africa and, as described below, research into environmental flows for rivers was advancing beyond the groundwork laid during the preceding decade.

1.1.3 Evolution of environmental flow science in South Africa

Early approaches to set environmental flows

The first documented South African attempt to address environmental flows can be traced back to the 1970-1980s, when the likely impacts of Pongolapoort Dam on the Pongola River were investigated and recommendations made for managed flood releases to maintain the flooding regime of floodplain pans (Coke 1970; Phélines *et al.* 1973; Heeg and Breen 1982). Shortly thereafter, a DWAF engineer, Roberts (1983), in projecting freshwater demands in South Africa, introduced an estimate of 11 % of the total water requirements of all sectors in the year 2000 for conservation purposes (O'Keeffe 1995). Although acknowledged at the time as simplistic and limited (based on the needs of only estuaries, lakes and nature conservation areas, but including maintenance of riverine habitats), it introduced the country's engineering

community to the idea of allocating water for environmental purposes and proved a catalyst for environmental flow research (King and Tharme 1994; Tharme 1996).

In 1987, two multidisciplinary workshops on environmental flows were held. The first was intended to assist DWAF in making decisions on future water allocations in the then eastern Transvaal, an area which encompassed some of the most socio-economically disadvantaged people of South Africa and the Kruger National Park, a premier conservation area (Bruwer 1991). The other more general workshop was designed to bring together, and assess the relevant knowledge of, the wider national community of river scientists, water resource engineers and managers, most of whom though experts in their respective disciplines knew little of environmental flow theory and practice (Ferrar 1989). The workshops generated two conceptual approaches for arriving at preliminary environmental flow estimates (King and O'Keeffe 1989), but no coordinated efforts were made to develop or formally apply environmental flow methodologies (EFMs) at that time (King and Tharme 1994).

Testing the Instream Flow Incremental Methodology for local application

The first full-scale local initiatives to address the EFRs of South African rivers commenced in the early 1990s, as two parallel, multidisciplinary research projects on environmental flows, funded by the South African Water Research Commission. They capitalized on the earlier workshops and a visit to South Africa by an expert in the most commonly applied approach globally at that time, the North American Instream Flow Incremental Methodology (IFIM), during which IFIM was tested locally (Gore and King 1989).

One of the projects, entitled "Assessment of the Instream Flow Incremental Methodology and initial development of alternative instream flow methodologies for South Africa" involved King and Tharme (1994) undertaking the first comprehensive assessment of the potential for routine application of IFIM in South Africa, using the Olifants River, Western Cape, as a test case. Further international exchange and training of South African researchers in IFIM (King and Tharme 1994; King *et al.* 1995), coupled with the second initiative, to address the EFRs of the rivers flowing through the Kruger National Park, within the Kruger National Park Rivers Research Programme, using a range of approaches including IFIM (O'Keeffe *et al.* 1987; O'Keeffe and Davies 1991; O'Keeffe 1995; King *et al.* 1995; O'Keeffe *et al.* 1996) gradually advanced the science locally.

The IFIM, and particularly its component software, Physical Habitat Simulation (PHABSIM), focus on quantitative relationships between instream physical habitat and discharge for individual target species (most commonly economically important salmonids) (Section 1.5). As the methodology allows for fairly limited links with both the hydrological regime of the study river and the responses of biota to changes in flow, it provides little indication of which of a suite of flow conditions might represent unacceptably high degrees of physical disturbance. Furthermore, PHABSIM, as a management tool, did not evolve conceptually from any grounding in disturbance or other ecological theory (R.T. Milhous, Instream Flow Group, Fort Collins,

U.S.A., pers. comm.; Stalnaker *et al.* 1994). Gore *et al.* (1990), however, inferred that IFIM was based on several of the conceptual precepts preceding the advent of hydraulic stream ecology (Section 1.4.8). It was concluded by King and Tharme (1994) for such reasons, that IFIM could not provide the kinds of recommendations on appropriate modified flow regimes urgently required to prevent further degradation of local rivers (Section 1.5.6). Moreover, in South Africa, the emphasis was necessarily directed at the maintenance of freshwater habitat rather than of individual species, due to major gaps in hydrological, geomorphological, and ecological understanding, and the lack of sufficient resources to resolve them (O'Keeffe 2000).

Although IFIM was found to be deficient in several areas that limited it for routine local application (see King and Tharme 1994, and Tharme 1996, for critiques), use of the methodology was instrumental in re-focusing the multidisciplinary thinking and research of South African practitioners in hydrology, hydraulics and river ecology on novel approaches to environmental flows (see below). It also resulted in more attention being given to studies of the interrelationships among flow, physical habitat and ecological response (e.g. Tharme and King 1998; Jewitt *et al.* 2001; King and Schael 2001; O'Keeffe *et al.* 2002; this thesis; Section 1.1.4).

Development and establishment of a new methodology: the Building Block Methodology

During the initial stages of the above research, growing collaboration between Australian and South African ecologists resulted in a joint conceptual framework being laid out at an international seminar and workshop on environmental flows, for a new direction in environmental flow science where the needs of the whole riverine ecosystem were addressed (Arthington *et al.* 1992; Section 1.5). In South Africa, the tenets of the holistic approach provided the impetus for the development of an alternative methodology to IFIM, and King and Tharme (1994) concluded their research with a first description of this new Building Block Methodology (BBM).

Through a series of environmental flow assessments for key South Africa rivers from the early 1990s onwards, spearheaded by the DWAF and supported by a national team of river scientists and water managers, the BBM evolved from its early origins to become the structured standard methodology for local application detailed in King and Louw (1998), King *et al*. (2000) and Hughes (2001) (Section 1.5). Interestingly, the existence and demonstrated successful use of a scientifically and legally defensible, as well as locally appropriate, methodology to quantify environmental flows was a key factor in the inclusion in legislation of the requirement for a statutory allocation of water to the resource itself (Palmer 1999).

1.1.4 Need for supporting research on flow-ecology relationships

On the basis of King and Tharme's (1994) findings, a follow-up WRC project "Development of the Building Block Methodology for instream flow assessments and supporting research on the effects of different magnitude flows on riverine ecosystems" was designed. Its main objectives were to continue development

of the BBM and support the growth of South African expertise in environmental flows, as well as to initiate research to test the validity of some of the guiding principles and assumptions underpinning the methodology and produce data to enhance its application (Tharme and King 1998).

The BBM's guiding principles (derived from the concepts expressed in Arthington *et al*. (1992), echo those later formalized as elements of the 'natural flow paradigm' by Poff *et al*. (1997) (Section 1.4) and were as follows (after Tharme and King 1998):

1. The biota associated with a river can cope with low (or zero) flow conditions that occur often naturally, and may be reliant on higher flows that naturally occur in it at certain times (e.g. specific floods), having evolved life history strategies that respond to natural flow regimes. Hence, hydrological events that are a 'normal' characteristic of a specific river, no matter how variable, unpredictable or biophysically stressful they may be, are ones to which the species and other components typical of that system are adapted and on which they may be reliant.
2. Identification of what are felt to be the most important characteristics of the natural hydrological regime, and their incorporation as part of a recommended modified hydrological regime, will facilitate maintenance of the river's natural biota and processes. The closer the recommended regime mimics the natural hydrological pattern, the more likely it is that natural ecosystem character will be maintained.
3. Certain kinds of flow events are more influential for river channel geomorphology than others. Identification of such flows and their incorporation into the modified flow regime will aid maintenance of the natural channel and river structure, and areal extent and diversity of different physical habitats that support the biota.

Discussions among South African river ecologists in developing the BBM relied on the above principles in focusing on which elements of the flow regime might be most critical to retain in a recommended modified flow regime (Section 1.5) for various river types (Tharme and King 1998); an example for a local river type is provided in Figure 1.1.

Essentially, the BBM (and other holistic environmental flow approaches; Section 1.5) hinges on a fundamental understanding of the processes governing river ecological integrity, accumulated as a wide-ranging body of theory (Section 1.4). Disturbance theory, in particular, was recognised as central to the methodology's foundation (King and Tharme 1994; Tharme and King 1998). In this regard, King and Tharme (1994) identified a clear need for improved understanding of the various interrelationships between ecology and hydrology, as well as of the effects of flow-related disturbance on the riverine ecosystem and its biota, in order to advance the BBM's scientific underpinnings. Research subsequently undertaken by Tharme and King (1998), including the low flow study presented in this thesis, was aimed at helping fulfil that need. At that time in South Africa and indeed globally, as is still the case, the science of ecohydrology was in its infancy and little attention in freshwater ecology had been devoted to the exploration of specific relationships between the characteristics of particular flow regimes or events, and ecological responses.

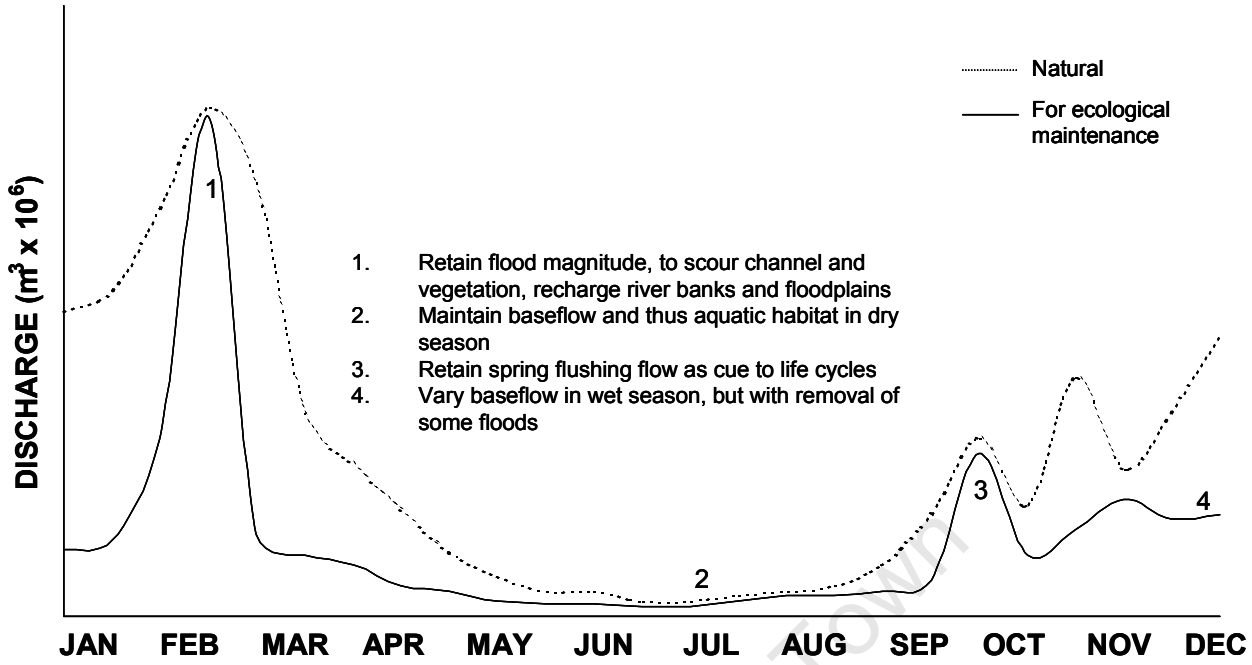


Figure 1.1 The natural flow regime of a hypothetical perennial river in central Natal, and those parts of it deemed most important for ecological maintenance should the flow regime be modified for human use (from Tharme and King 1998).

1.2 THESIS OBJECTIVES AND STRUCTURE

Given the need for intensified local research in ecohydrology, particularly in relation to holistic approaches to environmental flow determination (Section 1.5), this thesis aimed to identify and understand low flow events that constituted various degrees of physical disturbance to benthic macroinvertebrates as a key component of perennial lotic biota. It was envisaged that some of the links between changes in low flow regime, physical habitat, and biotic response could be elucidated, both to facilitate prediction of the potential ecological consequences for invertebrates of a given discharge and to better characterize ecologically relevant low flows for invertebrates, for potential application in future environmental flow studies.

The body of river ecological theory outlined below (Section 1.4) provided what was deemed a suitable basis for the development and testing of hypotheses on the relationships between flow, hydraulic habitat, and invertebrate response. Emphasis was placed on the short-term, small-scale direct impacts of low flows, or effects mediated through changes in physical habitat and/or water quality, on invertebrates, but with reference to the longer-term hydrological disturbance history of rivers. The extent to which the findings on invertebrate responses to changes in flow might benefit ecohydrological models within current environmental flow approaches was also examined.

1.2.1 Research hypotheses and main objectives

The research conducted in this thesis centred on two hypotheses:

1. Detectable relationships exist between the composition of benthic macroinvertebrate assemblages in perennial rivers and the flow-related quantity and quality of instream physical habitat, and these relationships can be used to identify characteristic responses of invertebrates to low flows.
2. There are degrees to which natural and unnatural low flow events constitute physical disturbances to invertebrates, which are a function of assemblage composition, physical habitat conditions, and a river's characteristic hydrological regime.

The associated main objectives were to:

1. Characterize low-flow disturbance histories for the rivers, and identify flow indices of potential ecological relevance.
2. Identify any indirect impacts on invertebrates resulting from short-term changes in water chemistry at natural and unnatural low flows.
3. Establish relationships between changes in the quantity and quality of instream physical habitat and natural and unnatural low flows.
4. Identify characteristic responses of invertebrate assemblages and taxa to short-term natural and unnatural low flows, and associated physical habitat dynamics.
5. Identify the flow-related physical habitat variables of most importance in determining the distributions and abundances of invertebrates, and determine the relationships between these variables and assemblage composition.
6. Determine the tolerance ranges of invertebrate assemblages and taxa for flow-related physical habitat variables of potential ecological relevance, and identify any taxa that are particularly sensitive to or tolerant of flow reduction.
7. Characterize ecologically relevant low flows for invertebrates, by linking key flow indices with invertebrate responses to, and physical changes in, habitat conditions at low flows.
8. Explore the implications of any characteristic relationships between low flow regime, habitat conditions, and invertebrate response, for the body of theory on disturbance and ecohydrology, particularly as applied in environmental flow science.

1.2.2 Thesis structure

The sequence of thesis chapters, their interrelationships, and the main objectives and corresponding research components addressed in each chapter are outlined in Figure 1.2.

The remainder of Chapter 1 sets the background on the current state of river hydrological alteration globally and its effects on riverine biota, before introducing the areas of stream ecosystem theory most pertinent for this thesis in terms of hydrology-ecology interactions. The final section, which sets the context for the potential application of the thesis findings for environmental flow assessment, incorporates the principal

literature review undertaken for this thesis, on the status of environmental flow assessment globally (Tharme 2003) and introduces some of the methodologies of particular relevance for determining invertebrate low flow requirements. Chapter 2 describes the study area and a pilot dry-season survey undertaken to identify suitable sites for the low flow research. Chapter 3 continues the methodology description, with a discussion of the overall design of the study and of the methods employed to examine the effects of natural and artificially manipulated dry season flows on benthic macroinvertebrates. Examination of the degree of natural hydrological similarity among the study sites (and hence, comparative flow disturbance histories), and of the extent to which the manipulated low flows were lower than natural discharges, forms the basis of Chapter 4. Low flow indices of potential ecological relevance were also identified. In Chapter 5, the extent to which changes in water chemistry at very low flows might have influenced biotic response, in the short-term, is addressed. In Chapter 6, the nature of the relationships between physical habitat and low flows is investigated at length, and at several scales of relevance to invertebrates and for environmental flow studies, with an emphasis on biotope characterization and patch dynamics. Invertebrate response to the low flow regime, including at biotope and microhabitat levels, forms the basis of the next Chapter 7, while in Chapter 8, an effort is made to consolidate the various biophysical responses to low flows, so as to characterize ecologically meaningful low flows for invertebrates. The final Chapter 9 provides a summary of the low flow research and describes future work. The implications of the thesis findings for ecohydrological theory as applied in river flow management are explored therein.

1.3 ALTERATION OF RIVER HYDROLOGICAL REGIMES: STATUS AND ECOLOGICAL IMPLICATIONS

1.3.1 Global availability and use of water resources

Existing and projected future increases in water demands have resulted in an escalating conflict between the development of rivers as water and energy sources and their conservation as biologically diverse, structurally and functionally integrated ecosystems (Gleick 1993; Abramovitz 1995; Postel 1998; The World Conservation Union (IUCN) 2000; Green Cross International (GCI) 2000; McCully 2001; Rosenberg *et al.* 2000; Postel and Richter 2003; Poff *et al.* 2003; Millennium Ecosystem Assessment (MA) 2005; Dudgeon *et al.* 2006; Richter *et al.* 2006; Molden 2007). Historically, the emphasis in developing and managing basin water resources has been on securing and maximizing a stable delivery of water with a high level of spatial and temporal predictability, to meet areas of human socioeconomic demand (Petts 1996; Richter *et al*. 2003, 2006). Past assessments of global water availability and scenarios for future water supply have addressed whether or not human needs can be met by the total renewable water resources in a country or basin (e.g. Rijsberman 2000; Shiklomanov 2000a, b; Vörösmarty *et al.* 2000; Rosegrant and Cai 2002). The interconnectedness of rivers, other wetlands, and water resources within the hydrological cycle has been poorly recognized (Falkenmark 2003), with inadequate consideration of the flow requirements of rivers and those communities directly dependent on them for their livelihoods (Baron *et al.* 2002; Naiman *et al.* 2002; Postel and Richter 2003; MA 2005).

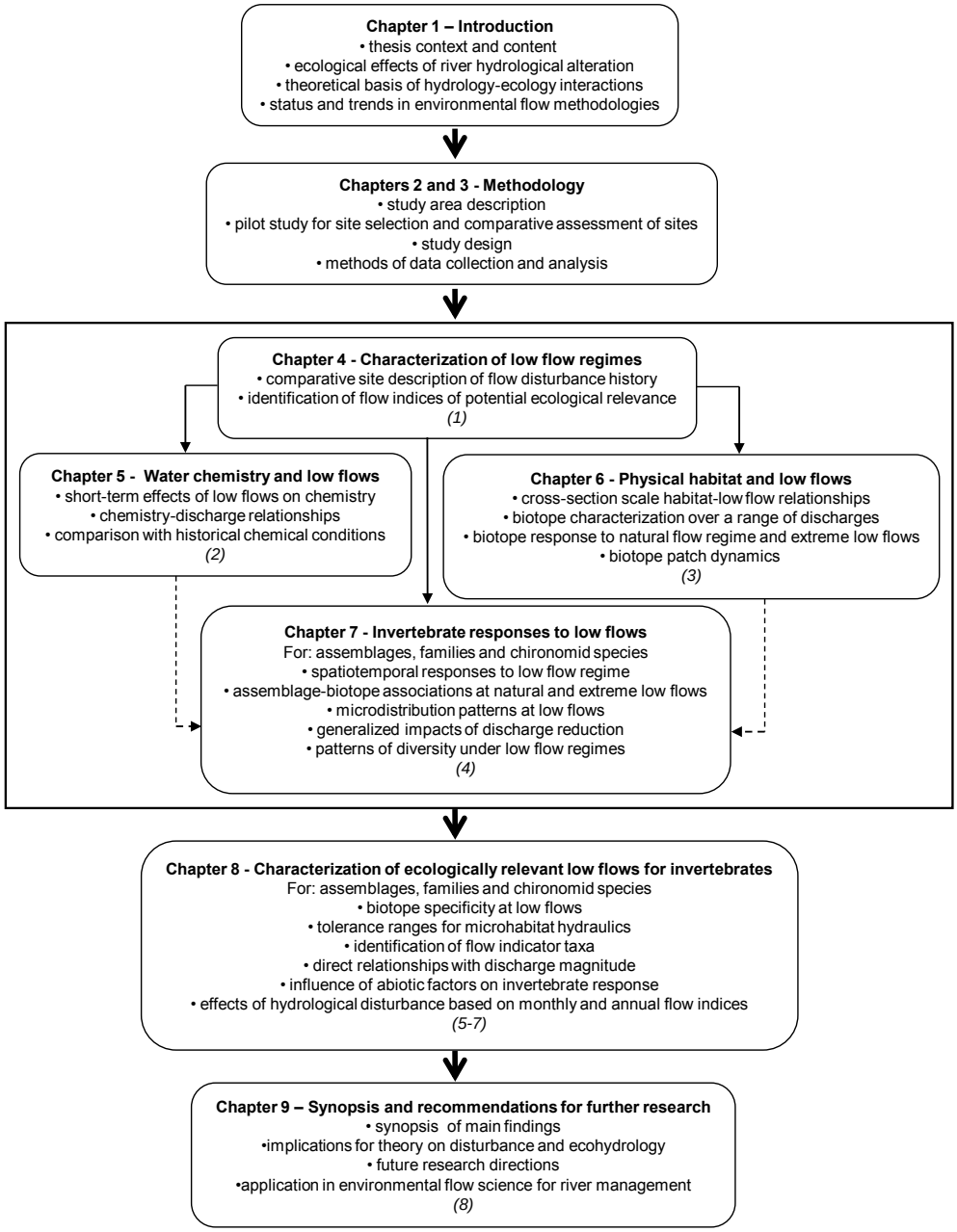


Figure 1.2 Schematic of the main thesis components covered in each chapter with the number(s) of the corresponding objective(s) addressed in italics (below, in parentheses). Thick solid arrows depict the main sequence of steps. Thin solid arrows indicate direct relationships among the key factors considered, while dotted arrows indicate indirect links. The group of potential disturbance effects and biophysical responses within the rectangle were combined for the approach described in Chapter 8.

Although a precise inventory of global water demand and supply does not exist, a review of available data sources indicated global water withdrawal in the order of 4000-5000 km^3 y^{-1} (Gleick 2000; Vörösmarty and Sahagian 2000; United Nations World Water Assessment Programme 2006). Relative to the estimated 40 000 km^3 y^{-1} global supply of renewable water, such use represents 10-15% of current water supply

(Shiklomanov 1997, 2000a). Of this small proportion of global runoff, only 31% is readily utilisable in terms of its spatiotemporal distribution (Postel *et al.* 1996). Presently, 54% of this accessible surface water is already appropriated by humans and this is projected to increase to 70% by 2025, to cope with growing competitive demands, coupled with an increase in world population to around eight billion (Postel *et al.* 1996; Postel 1998; Vörösmarty and Sahagian 2000). Close on 40% of the world population currently experiences serious water shortages (Gleick 1993, 2000; Richter *et al*. 2003) and at least 3.5 billion people will inhabit water-stressed river basins by 2025 (Revenga *et al.* 2000). Moreover, the per capita availability of water globally is predicted to decline to approx. 5000 m^3 a^{-1} by 2025, exacerbating an existing negative trajectory from 16 000 (in 1950) to only 6700 m^3 a^{-1} in 1998 (World Resources Institute, WRI, 1998; Shiklomanov 2000a, b). Such downward trends in water resources sustainability have lead to enormous pressure being exerted on rivers, with grave implications for ecosystem protection and future resource management (see below). Smakhtin *et al*. (2004) estimated that over 1.4 billion people currently live in basins with high environmental water stress (covering 15% of the world's land surface), a number that is likely to escalate if water withdrawals continue to increase without secured allocations to redress the balance between the water needs of ecosystems and other sectors (Section 1.5).

1.3.2 State of alteration of river flow regimes

Water resource developments and their associated hydraulic infrastructure (e.g. dams, diversion weirs, IBTs, run-of-river abstraction, and aquifer exploitation) aimed at matching water supply with demand for agriculture, hydropower generation, industry and domestic supply, are ubiquitous and already responsible for unprecedented multi-scale effects on riverine ecosystems (Richter *et al*. 2006). The majority of such detrimental impacts have emanated from restructuring of the hydrological regimes on which river ecological character fundamentally depends (Ward and Stanford 1979; Rosenberg *et al.* 2000; Nilsson and Berggren 2000; Vörösmarty and Sahagian 2000; Baron *et al*. 2002; Richter *et al*. 2003; Section 1.4). In many instances, changes in catchment land use have further contributed to flow alteration (Poff *et al.* 1997, 2006a, b).

Hydrological alteration of river systems, defined by Rosenberg *et al.* (2000, p. 747) as "any anthropogenic disruption to the magnitude or timing of natural river flows" is now a global phenomenon of staggering proportions (Postel and Richter 2003). Flow regulation through impoundment represents by far the most prevalent form of hydrological alteration worldwide with, according to recent estimates which remain incomplete, well over 45 000 extant large dams in over 140 countries (WCD 2000). These dams, some two thirds of which are in the developing world, impound at least 14% of world runoff, with an estimated 8400 km^3 of water in storage, and have proliferated by a factor of seven since 1950 (L'vovich and White 1990, cited in Revenga *et al.* 2000; Vörösmarty *et al.* 1997; Nilsson *et al.* 2005). A further 800 000 small dams are estimated to exist worldwide, in all likelihood a gross underestimate (Adams 1991; Rosenberg *et al*. 2000; McCully 2001). Although dam building peaked in the 1970s and construction rates are in decline, water-resource development continues unabated, particularly in developing regions, with an estimated average of

160-320 new large dams being constructed annually worldwide (WCD 2000; Revenga *et al.* 2000; McCully 2001; Richter *et al*. 2006). Many such dams threaten the integrity of some of the few remaining unregulated rivers of the world.

Studies of the world's large river systems (LRSs – systems with a river channel section of virgin mean annual discharge, VMAD $\geq$ 350 m^3 s^{-1} anywhere within the catchment), representing 60% of world virgin runoff, have shown that at least 59% (172 out of 292) are fragmented by flow regulation and channel fragmentation associated with dams, including the eight most biogeographically diverse systems (Dynesius and Nilsson 1994; Revenga *et al.* 1998, 2000; Nilsson *et al.* 2005). Thirty-six percent of the LRSs were strongly affected (Nilsson *et al.* 2005); strongly fragmented rivers were characterised as having less than 25% of the main channel unimpounded, substantial alteration of their annual flow patterns, and/or where the largest tributary possessed at least one dam. Forty-one percent of the systems examined had intact tributaries, while 48% remain non-fragmented by dams in the main channel. Australia, for example, was found to contain the highest proportion of unaffected systems. Europe had the fewest unaffected systems (Nilsson *et al.* 2005), with the European Union regulating the flow of 60-65% of the rivers in its territories (Zwick 1992; WCD 2000). In Asia, just under half of all regulated rivers possess more than one dam (WCD 2000) and flow regulation percentages have reached 130% (Dudgeon 2000; Nilsson *et al.* 2005).

Across world regions, several large rivers are over-abstracted to the point that essentially no water reaches the sea (e.g. McCully 2001; Postel *et al*. 1996; Postel 1995; Revenga *et al.* 1998, 2000; Thoms and Sheldon 2000; MA 2005). In addition to an overall reduction in the quantity (and quality) of river water, in several instances, particularly with IBTs, flow has been increased above natural levels for certain periods of the year and/or flow variability has been significantly dampened (e.g. Snaddon *et al*. 1999). Vörösmarty *et al.* (1997) and Vörösmarty and Sahagian (2000) demonstrated that the world's population of large dams has caused considerable ageing in river runoff, which in turn reflects increased biophysical disturbance to the natural system. Computed runoff ageing signatures for 236 regulated rivers showed that the mean age of their water is two to four times greater by the time the coastal zone is reached than for free-flowing systems, with several large rivers experiencing a reservoir-induced ageing in excess of three months (Covich 1993; Vörösmarty *et al.* 1997, 2000).

1.3.3 Effects of altered flow regimes on riverine ecosystems and biodiversity

Although limited in global habitat extent, riverine ecosystems are diverse in character and relatively species rich, supporting a disproportionately large number of species of certain taxonomic groups and exhibiting high endemism levels (Allan and Flecker 1993; Groombridge and Jenkins 2002; Revenga and Kura 2003; Dudgeon *et al*. 2006). The relative species richness of freshwater systems, based on the ratio between species richness and habitat extent, at 3.0, exceeds that for terrestrial (2.7) and marine (0.2) ecosystems (MA 2005). Currently, however, river degradation and loss are also greater than that recorded for other ecosystems globally, with the concomitant deterioration in aquatic biodiversity attributed principally to a

few, interacting drivers that include flow modification and associated changes in water quality and habitat condition (MA 2005; Dudgeon *et al*. 2006). The Living Planet Index, an aggregate index of trends in marine, freshwater and terrestrial vertebrate species populations, showed that freshwater populations have declined consistently and more drastically than marine or terrestrial ones, with an average decline of 50% between 1970 and 2000; over the same period the other groups decreased by a significant, but lesser 30% (MA 2005).

The deterioration of many groups of riverine-dependent fauna and its connection to flow alteration are described in Pringle (2000), Revenga *et al*. (2000), Revenga and Kura (2003), Postel and Richter (2003), MA (2005), and Dudgeon *et al*. (2006). More than 20% of the world's 10 000 described freshwater fish species have been listed as threatened, endangered or extinct in the last few decades (Pringle 2000) and at least half of its 200 freshwater turtle species are globally threatened, reaching 75% for Asia (MA 2005). Allan and Flecker (1993) identified habitat loss and degradation, principally through alteration of river flow regimes, as one of six major factors globally threatening the destruction of lotic ecosystems and species. It has been well documented, for example, that altered hydrologic regimes represent one of the three leading national threats to the imperilment of freshwater fauna in the U.S.A. (Richter *et al.* 1997b), as well as the principal cause of decline of the native fish fauna of California (Moyle and Williams 1990). Alteration of natural flow regimes also remains one of the three most serious threats to the conservation of riverine biodiversity in tropical Asia, a region that houses a disproportionately high amount of global aquatic biodiversity and where that biodiversity is in serious decline (Dudgeon 1992a, 2000). Projections indicate a global freshwater 'biodiversity crisis' with continuing declines in freshwater biodiversity (Abell 2002; MA 2005). Extinction rates for North American freshwater fauna alone have been projected at 4% per decade, five times higher than terrestrial species losses (Ricciardi and Rasmussen 1999).

Certainly, considerable evidence exists that the alteration of a river's hydrological regime from its natural state constitutes arguably the major physically adverse disturbance to the ecosystem and its biodiversity, and that such disturbance is legion at local to global scales (Postel and Richter 2003; Dudgeon *et al*. 2006). It has provided much of the impetus for numerous flow restoration initiatives across the globe (Bunn and Arthington 2002; Postel and Richter 2003), even leading in some instances to decommissioning of hydraulic infrastructure (McCully 2001). Richter and Richter (2000, p. 1468) observed that interestingly, in several instances, the latter adaptive management experiments have led to "significant departures from long-held, narrow perceptions about the range of flows needed to sustain riverine biota". Both upstream and downstream detrimental ecological effects occur as a result of flow alteration and fragmentation, some of the most serious of which may be far removed in time and space from the flow-impact source or unanticipated (Petts 1980, 1987; Allan and Flecker 1993). Furthermore, declines in biodiversity, ecosystem integrity and resilience have diminished the capabilities of rivers to deliver the myriad ecosystem services (*sensu* MA 2005) vital to human wellbeing, with attendant increased social and economic costs (Postel 1998; Acreman *et al.* 2000; Baron *et al*. 2002; Richter *et al*. 2003; Molden 2007).

Petts (1989) identified three orders of impact of streamflow regulation on rivers: first order impacts that are immediate and affect the flow regime, sediment transport, water quality, temperature and energy transfers; second order impacts which include changes to channel geomorphology and primary production that can extend over 1-100 years; and third order impacts, which reflect all the changes brought about by first- and second-level effects and affect instream communities (with variable, potentially lengthy delays). The ecological effects manifested may be in response to changes in one or a complex combination of flow regime and other key ecological attributes (Section 1.4). They may also act synergistically, accounting for a far greater detrimental impact on the system than in isolation. Lake (2003) highlighted the importance of the four-dimensional and spatiotemporally heterogeneous nature of lotic ecosystems (Ward 1989) when assessing impacts on hydrological connectivity. Pringle (1997) too emphasised greater consideration of the ways in which effects of flow disturbances in lower reaches can result in linked, upstream transmission of impacts to upper rivers, potentially with lag times and resultant upstream legacies.

It is beyond the intent of this thesis to review the plethora of literature substantiating the incontrovertible ecological and geomorphological effects and knock-on socioeconomic implications, of hydrological alterations on riverine ecosystems and their biota at genetic, ecosystem and global scales (Rosenberg *et al.* 2000). Impacts have included declines in the biodiversity of species groups, genetic isolation through habitat fragmentation, changes in processes such as nutrient cycling and primary productivity, altered chemical and thermal regimes, decreased functioning and altered structure of riparian zones, channel form change and coastal erosion, altered food webs, as well as declines in floodplain fisheries and other ecosystem services. Much of the evidence of such inimical biophysical consequences of hydrological alteration is based on comparative assessments of regulated and unregulated rivers, and numerous regional and country-specific discussions of the topic exist. Moreover, even in countries where there has not been extensive research on the topic historically, there is a growing body of evidence connecting the decline of riverine systems and biota with flow alteration. General examination and syntheses of the range of effects of flow alteration are presented in: Ward (1976); Ward and Stanford (1979); Brooker (1981); Ward (1982); Petts (1984a); Lillehammer and Saltviet (1984a); Armitage (1995); Cushman (1985); Craig and Kemper (1987); Gore and Petts (1989); Voelz and Ward (1989); Calow and Petts (1992); Boon *et al.* (1992, 2000); Power *et al.* (1996); Rosenberg *et al.* (1997, 2000); Poff *et al.* (1997); Richter *et al.* (1997a); Bragg *et al.* (1999); Snaddon *et al.* (1999); Nilsson and Berggren (2000); Pringle *et al.* (2000); Pringle (2000); WCD (2000); Bergkamp *et al.* (2000); Jansson *et al*. (2000); Welcomme (2001); Bunn and Arthington (2002); Postel and Richter (2003); and Dudgeon *et al*. (2006). These various sources provided much of the evidence on which the estimate is founded that more than half the world's rivers have been detrimentally affected ecologically by hydrological regulation (WCD 2000).

In a focused review of the ecological consequences of altered flow regimes for aquatic biodiversity, Bunn and Arthington (2002) identified a range of biotic responses under broad areas of flow-related impact (Table

1.1). Supported by this evidence, Bunn and Arthington (2002) elaborated four guiding principles on the influence of river hydrology on aquatic biodiversity, and the consequences of changing flow regimes in each instance. Three of these, especially principle (1), are of relevance for this thesis: (1) flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition; (2) aquatic species have evolved life history strategies primarily in direct response to the natural flow regimes; (3) maintenance of natural patterns of longitudinal and lateral connectivity is essential to the viability of populations of many riverine species; and (4) the invasion and success of exotic and introduced species in rivers is facilitated by the alteration of flow regimes.

Table 1.1 examples were selected from an enormous diversity and number of documented cases of biotic response to flow change, and provide a useful point of departure for understanding flow-ecology relationships. Similar examples can be found for geomorphic flow-related impacts on rivers (e.g. WCD 2000), of which only those impacts on reach instream habitat at dry-season low flows are considered in this thesis, from the perspective of the benthos (Section 1.2; Chapter 6). A specific overview of the effects of altered low flows on benthic macroinvertebrates forms the introduction to Chapter 7.

1.4 LINKING HYDROLOGY AND ECOLOGY: A THEORETICAL BASIS

The irrefutable evidence that hydrological alteration has caused detrimental changes to riverine ecosystems and biodiversity (Section 1.3) reflects the central importance of and wide range of roles played by a river's flow regime. There remains quite rudimentary quantitative understanding, however, of the specific ecological and geomorphological functions that different elements of the flow regime naturally perform in a river, and across different systems, and of the ecological responses brought about by alterations from natural in individual flow elements (Poff *et al.* 1997; Tharme and King 1998; Puckridge *et al.* 1998).

1.4.1 Ecohydrology – a rapidly evolving discipline

Petts *et al.* (1995) reviewed advances made in linking hydrology and ecology over the past century, particularly in the context of stream ecosystem theory as elaborated by Minshall (1988), and explained why connections between these two areas of science were limited prior to the 1970s. They highlighted conceptual thinking from hydrology and its allied discipline, geomorphology, that was fundamental in taking forward modern river ecology, notably that pertaining to spatial and temporal scales (Minshall 1988) and energy equilibrium theory (e.g. as adapted by Vannote *et al*. 1980). It was only by the late 1980s, according to Petts *et al.* (1995), that lotic ecologists had developed and subjected to testing theoretical models believed to govern river structure, functioning and response to anthropogenically induced change (though capitalizing on the earlier descriptive and experimental research Minshall (1988) outlined). Theories that furthered understanding of hydrology-ecology interactions included: the river continuum concept (Vannote *et al*. 1980); serial discontinuity concept in river regulation (Ward and Stanford 1983a, 1995); nutrient spiralling hypothesis (Pringle *et al.* 1988; Davies and Day 1998); flood pulse concept for floodplain river systems

(Junk *et al.* 1989; Puckridge *et al.* 1998) and riverine productivity model (Thorpe and Delong 1994). Various disturbance theory and patch dynamics models also have contributed invaluable insights (see below).

Table 1.1 Examples of biotic responses to altered river flow regimes, in relation to four key areas of impact (adapted from Bunn and Arthington (2002), in which specific references are provided). *Some examples are based on studies of responses to variation in natural flow regimes.

FLOW VARIABLES AFFECTED	BIOTIC RESPONSES
Flow induced changes in habitat	
Increased stability of baseflow and reduction of flow variability	Excessive growths of aquatic macrophytes
	Proliferation of nuisance larval blackflies
	Reduction in fish populations
	Increased standing crop and reduced diversity of macroinvertebrates
Erratic (diurnal) patterns in flow below hydroelectric dams	Reduction in species richness of benthic macroinvertebrates
	Reduction in standing crop of benthic macroinvertebrates
	Stranding of macroinvertebrates
	Stranding of fish
Conversion of lotic (flowing water) habitat to lentic (standing water) habitat	Decline of populations of riverine crayfish and snails
	Elimination of salmonids and pelagic spawning fishes and dominance of generalist fish species
	Loss of fishes adapted to turbid river habitats
	Loss of fishes due to inundation of spawning grounds
*Life history responses to altered flow regimes**	
Rates of water level fluctuation	Aquatic macrophyte growth rates and seedling survival
Timing of spates (floods)	Reduced survivorship of larval atyid shrimps following early summer spates
	Stable low flows required for spawning and recruitment of riverine fish
Reduced seasonality	Reduced synchrony of breeding in gammarid shrimps
Timing of rising flows	Loss of cues for fish spawning and migration
Short-term fluctuations in flows	Adverse effect on species of stoneflies with long larval development times (autumn/winter)
Modified temperature regimes below dams	Delayed spawning in fish
	Disrupted insect emergence patterns
	Reduced benthic invertebrate standing crop (component of fish diets)
	Elimination of temperature-specific species of fish
Loss of longitudinal or lateral connectivity of wetlands	
Water abstraction	Reduction in migrating shrimp larvae
Presence of in-stream barriers	Increased predation on juvenile migrating shrimp
	Loss of migratory fish species
Reduced frequency, duration and area of inundation of floodplain wetlands	Reduced spawning areas and/or recruitment success of lowland river fish
	Decline in waterbird species richness and abundance
	Decline in wetland vegetation
Invasion and success of exotic and introduced species	
Loss of wet-dry cycles and increased stability of water levels	Reduced growth and survival of native aquatic macrophytes and increased invasion of exotics
Reduced flow variability and increased seasonal stability	Favoured populations of exotic fish species (carp, mosquitofish)
Conversion of lotic to lentic habitat	Proliferation of exotic fish species
Interbasin transfers of water	Transfer of schistosomiasis; translocation of fish species

Building on such groundwork, contemporary river theory has evolved to better underpin and strengthen scientific understanding of the ways in which riverine ecosystems respond to flow-related environmental variability, gradually drawing together and combining hydrology, physical habitat-hydraulics modelling and community ecology within a single framework (Petts *et al.* 1995; Tharme and King 1998). Although debate surrounding the importance of flow regime variability in organizing and maintaining the ecological character of rivers, and on the potential use of flow-ecology relationships in river management, was vigorous over the past decades, the application of a unified, interdisciplinary branch of science to rivers remained neglected in practice (King and Tharme 1993; Dunbar and Acreman 2001; Naiman *et al*. 2002).

In the last decade, however, ecology-hydrology approaches have gained prominence, expanding exponentially in response to the need for more informed decision making in river management, particularly in situations where predictive understanding of the flows required to sustain natural river processes is limited (Poff *et al*. 2003, Arthington *et al*. 2006; Section 1.5). Zalewski (2000, p. 1) formally coined the term 'ecohydrology' as "the study of the functional interrelations between hydrology and biota at the catchment scale". Janauer (2000) and Zalewski (2002) highlighted the need to integrate quantitative hydrological data with ecological concepts and modelling, with due attention to issues of scale, to support water resources management, including through the use of ecosystem processes as management tools. Similarly, Dunbar and Acreman (2001, p. 1) identified applied hydro-ecology as "the linkage of knowledge from hydrological, hydraulic, geomorphological and biological/ecological sciences to predict the response of freshwater biota and ecosystems to variations of abiotic factors over a range of spatial and temporal scales." Essentially, the two concepts overlap, nested within the framework of IWRM (Naiman *et al*. 2006), and are treated synonymously in this thesis. Increasingly too, the distinction between hydroecology (or ecohydrology) and fundamental aquatic ecology is becoming less apparent (Dunbar and Acreman 2001) or indeed meaningful (Hannah *et al*. 2004; Chapter 9). It might well be argued that ecohydrology now possesses an established conceptual foundation centred on the tenets of the natural flow paradigm (Section 1.4.2), comprising a novel combination of disturbance theory, habitat template and patch dynamics concepts, fluvial geomorphic theory and ecohydraulics (Sections 1.4.3-1.4.8).

1.4.2 Character and ecological importance of the natural hydrological regime

Flow as a master variable - the natural flow paradigm

Since the founding work of Hynes (1970), albeit largely implicitly, there has been the recognition that the natural flow regime of a river and its inherent variability are central to sustaining native biodiversity and ecosystem integrity (Poff and Ward 1989; Karr 1991; Walker *et al.* 1995; Richter *et al.* 1997a; Stanford *et al.* 1996; Puckridge *et al.* 1998; Hart and Finelli 1999; Rosenberg *et al.* 2000; Naiman *et al*. 2002), and that "modification of flow thus has cascading effects" on river integrity (Poff *et al.* 1997, p. 770).

Riverine ecosystems require their natural flow regime in all of its temporal and spatial variability to maintain their natural ecological integrity and processes, and long-term evolutionary potential (Bunn and Arthington 2002; Arthington and Pusey 2003; Olden and Poff 2003; Lytle and Poff 2004). Certainly, it is an increasingly held view that without the maintenance or restoration of some semblance of natural flow variability in flow-impacted systems, it is not possible to effectively conserve riverine ecosystems or biota (Arthington *et al*. 1992; Walker *et al*. 1995; Stanford *et al*. 1996; Richter *et al.* 1996, 1997a; Tharme and King 1998; Bunn and Arthington 2002; Baron *et al*. 2002). As Poff *et al*. (2006a, p. 149) observed "The importance of hydrologic variability in sustaining natural riverine ecosystems is now well accepted".

The hydrological regime of a river can be considered a 'master variable' (Chapter 4), driving critical elements of ecosystem structure and processes that determine system integrity, as well as the distribution and abundance of riverine species (Poff and Ward 1989; Resh *et al*. 1988; Karr 1991; Stanford *et al.* 1996; Poff *et al.* 1997; Richter *et al.* 1996, 1997a; Puckridge *et al*. 1998; Baron *et al*. 2002). Richter *et al.* (1997a, p. 233) stated that current knowledge of the interrelationships between hydrological variability and ecosystem integrity provided firm evidence for a 'natural flow paradigm' where: "the full range of natural intra- and inter-annual variation of hydrological regimes, and associated characteristics of timing, duration, frequency and rate of change, are critical in sustaining the full native biodiversity and integrity of aquatic ecosystems." The five components of the flow regime widely considered most influential, namely the magnitude, frequency, duration, timing and rate of change of hydrologic conditions, are described in Table 1.2. These components can be used to characterise the entire spectrum of variability in flow, including average flow conditions, intra-annual or inter-annual variability, as well as to define individual common and extreme hydrologic events across the continuum from low flow to high flow events (Poff *et al.* 1997). Quantitative assessment of these various elements of river flow is essential for comprehending and predicting the ecological effects of both natural and altered flow regimes on riverine biota (Petts *et al.* 1995; Tharme and King 1998; Olden and Poff 2003). As Richter *et al.* (1997a, p. 233) commented, "Translating the natural flow paradigm into management targets requires decomposing the temporal complexity inherent in a streamflow regime into ecologically meaningful and manageable parts".

The process of identifying the different components of a river's flow regime, so as to best mimic overall natural variability, can be complex from a hydrological perspective (e.g. defining what constitutes a small flood that occurs often, or a low flow that is below natural magnitude). Identification of which of the full spectrum of flow characteristics are the most ecologically relevant ones, however, remains perhaps the most challenging process (King and Tharme 1994; Poff 1996; Tharme and King 1998; Postel and Richter 2003; Olden and Poff 2003; Monk *et al*. 2006, 2007). In fact, that 'ecologically relevant flow events' can be elucidated and defined, that is that specific low and high flow events can be characterised in terms of their explicit relevance for various aspects of river ecosystem structure, biota and/or processes, is a central precept for the low flow research undertaken in this thesis (Section 1.2) and for the scientific basis of environmental flow assessment more generally (Section 1.5). Richter *et al.* (1996, p. 1164) lend full support to this

statement in saying "Effective ecosystem management of aquatic, riparian, and wetland systems requires that existing hydrologic regimes be characterized using *biologically relevant* hydrologic parameters, and that the degree to which human-altered regimes differ from natural or preferred conditions be related to the status and trends of the biota."

Table 1.2 Critical components of a river hydrological regime (adapted from Poff *et al.* 1997).

Component	Description	Examples
Magnitude	The magnitude of discharge (also termed 'streamflow', 'flow rate', or more ambiguously 'flow') represents, for any given time interval, the volume of water moving past a fixed location per unit time. Units of measurement may be absolute or relative, and may vary from near-instantaneous to longer-term units.	30.7 $m^3 s^{-1}$, 2 km^3 per year
Frequency	The frequency of occurrence (also expressed as return period for flood events) indicates how often a flow above a given magnitude occurs over a specific time period. It is inversely proportional to discharge.	1 in 5 year flood
Duration	The period of time associated with a specific flow condition. Duration may be defined relative to a particular event or as a composite expressed over a specified time period	5 day 1: 100 year flood event; 23 days above 5 $m^3 s^{-1}$
Timing	Timing (or predictability) refers to the regularity with which flows of defined magnitude occur. It can be defined with reference to various time scales, and informally or formally.	First flood event of the wet season, in early July
Rate of change	The rapidity with which flow changes from one magnitude to another is referred to as the rate of change of flow (or flashiness). It may range from extremely rapid for flashy rivers to slow for relatively stable river types.	Mimic natural hydrograph shape

Ecological importance of the natural hydrological regime

Poff and Ward (1989, p. 1805) observed that flow is "arguably the most characteristic physical attribute of stream ecosystems" and that "Because streamflow exerts control over many important structural attributes in streams (e.g. habitat volume, current velocity, channel geomorphology, and substratum stability), flow measures represent an integration of complex environmental conditions". Figure 1.3 indicates the five major ecological attributes influencing aquatic biota, and through which human-induced alterations are mediated, the leading one of which is the flow regime (Karr 1991). It illustrates the role of the natural flow regime in exerting influences on river ecological integrity either directly or indirectly through other primary regulators: physical habitat, water quality, energy (food) sources and biotic interactions (including feedback loops) (Karr 1991; Dynesius and Nilsson 1994; Poff *et al.* 1997; Mitsch and Gosselink 2000). Modification of any of the criteria comprising the flow regime, singly or synergistically, will result in some degree of impact on the riverine ecosystem (Section 1.3).

The precise relationship between flow and other elements of pattern and process in rivers varies among rivers and within a single system (Poff and Ward 1990). Riverine biota exhibit life history, behavioural and morphological modes of adaptation to flow regime events; Lytle and Poff (2004) provide a synopsis of such adaptations to droughts and floods. Life history adaptations typically involve synchronization of life cycle

events (e.g. growth, reproduction) with the long-term average dynamics of the flow regime, including flow variability and predictability, and the timing and magnitude of extreme low- and high-flow periods (Petts *et al.* 1995; Lytle and Poff 2004). Riverine organisms can also exhibit behavioural adaptations that enable them to immediately respond to individual extreme flow events, often through reaction to a correlated environmental cue, or particular morphological adaptations (Lytle and Poff 2004). Petts *et al.* (1995) and Bunn and Arthington (2002), cautioned, however, that the relationship between flow and the distribution of aquatic organisms may often be complicated by other factors that vary in significance according to scale. For instance, at catchment scale, hydrological factors may be secondary in influence to water chemistry, while local hydraulics may bear a more direct influence within a river reach.

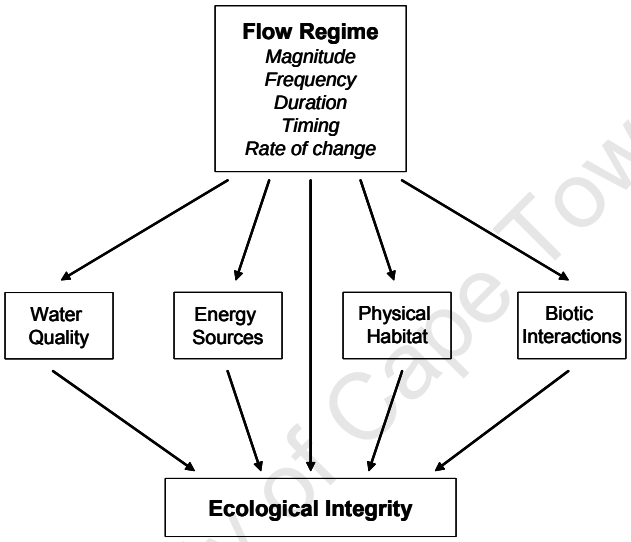


Figure 1.3 Direct and indirect influences of the hydrological regime on river ecological integrity (adapted from Karr 1991; Poff *et al.* 1997).

Roles of different flow events

A vast body of science has accumulated demonstrating the specific ways in which the flow regime of a river and its natural variability are of paramount importance in maintaining ecosystem condition and biodiversity, much of it gleaned through assessments of the detrimental impacts of altered hydrology on river ecology and geomorphology (Section 1.3; Minshall 1988; Resh *et al.* 1988; Poff and Ward 1989; Poff *et al.* 1997; Richter *et al.* 1997a; Rosenberg *et al.* 2000; Bunn and Arthington 2002). Less attention has been paid to how the different modes of adaptation exhibited by lotic organisms determine their degree of vulnerability to the impacts of altered flow regimes (but see Lytle and Poff 2004).

In countless ways river functioning is inextricably linked to the natural seasonal and between-year cycles of high and low flows (Petts and Maddock 1994; Postel and Richter 2003). Flow is known to be closely correlated with key physical and chemical characteristics in rivers, including rates of renewal of resources, hydraulics and temperature regime (Vannote *et al*. 1980; Poff and Ward 1990). The flow regime plays key

roles in regulating the stability and complexity of river channels, the import and export of allochthonous food and habitat resources, the activities and life cycles of biota, and so on. The ecological functions performed by different flow events are manifold, with examples presented in Table 1.3 and broad accounts provided in Gordon *et al.* (1992), Poff *et al.* (1997), Bunn and Arthington (2002), Postel and Richter (2003). There also is a considerable body of knowledge on the driving role played by hydrology in the interrelationships between fluvial geomorphological form and process (e.g. sediment transport), channel form and hydraulic habitat, impacts of flow regulation, and their geomorphological significance. Substantive accounts are provided in Petts (1980, 1984a, b); Gordon *et al.* (1992); Rosgen (1994); Stewardson and Gippel (1997); Rowntree and Wadeson (1998, 1999); Brizga (1998); and Rowntree (2000).

Emphasis has been given to the tremendous geomorphological and ecological significance, as well as the natural disturbance roles of higher flows, including freshes and intra- and inter-annual floods (e.g. Table 1.3). Not the focus of this thesis, specific examples are provided in: Williams and Winget (1979); Petts (1979, 1980, 1984b); Leathe and Nelson (1986); Reiser *et al.* (1987); Kondolf *et al.* (1987); Brittain and Eikeland (1988); Scrimgeour *et al*. (1988); Junk *et al.* (1989); Reiser *et al.* (1989a); Biggs and Close (1989); Palmer *et al*. (1992); Dudgeon (1993); Sparks (1995); Birkhead *et al*. (1996); Stromberg and Patten (1996);Biggs *et al*. (1997); Puckridge *et al*. (1998); King *et al.* (1998); Acreman *et al.* (2000); Kingsford (2000); Welcomme (2001); Bunn and Arthington (2002); Powell *et al*. (2002).

In contrast to the wealth of literature on floods, fewer studies document the specific ecological and geomorphological roles of low flows though several are intuitively understood (Tharme and King 1998; Rowntree and Wadeson 1998; e.g. Table 1.3). Most importantly perhaps, low flows define whether or not a river is naturally perennial or temporary, and the myriad implications deriving from this fundamental distinction (Williams and Hynes 1977; Poff and Ward 1989; Boulton and Suter 1986; Williams 1996; Uys and O'Keeffe 1997b; O'Keeffe and Uys 1998). Differences in dry- and wet-season low flows are critical in defining the seasonal requirements of different communities. Other vital provisions of low flows include: physical habitat of appropriate quality and diversity, and indirect influences on sediment transport and channel morphology (Wadeson 1994; Brizga 1998; Chapter 6), for species survival and maintenance; stable conditions for certain fish species to initiate and complete their reproductive cycles (Skelton 1993; Bunn and Arthington 2002) and for aquatic invertebrates to undergo cycles of rapid development, growth, and in many instances emergence as aerial adults (Hynes 1970); specific ranges in water temperature and chemistry which act as various biological cues (Malan and Day 2002a, b, Chapter 5); temporarily closed nutrient-cycling loops (Davies and Day 1998); the basic dry-season volume of water atop which freshes are generated (e.g. for flushing poor water quality from pools) (Tharme and King 1998); water to river banks, to maintain marginal and riparian vegetation (Birkhead *et al*. 1996); and water for wildlife and human consumption (Tharme 1996; Arthington and Zalucki 1998a).

Table 1.3 Examples of ecological functions performed by different river flow levels (adapted from Postel and Richter 2003).

FLOW COMPONENT	ECOLOGICAL ROLE
Low (base) flows	
Normal level:	Provide adequate habitat space for aquatic organisms
	Maintain suitable water temperatures, dissolved oxygen and other chemical conditions
	Maintain water table levels in floodplain and plant soil moisture
	Provide drinking water for terrestrial animals
	Keep fish and amphibian eggs suspended
	Enable passage of fish to feeding and spawning areas
	Support hyporheic organisms (living in saturated sediments)
Drought level:	Enable recruitment of certain floodplain plants
	Purge invasive, introduced species from aquatic and riparian communities
	Concentrate prey into limited areas to benefit predators
Higher flows (freshes or small floods)	Shape physical character of river channel, including availability and heterogeneity of different biotopes (e.g. riffles, pools) and microhabitats
	Restore normal water quality after prolonged low flows, flushing away waste products and pollutants
	Maintain suitable salinity conditions in estuaries
	Prevent encroachment of riparian vegetation into the channel
	Aerate eggs in spawning gravels, prevent siltation of cobble interstices
	Determine size of river bed substrata (sand, gravel, cobble, boulder)
Large floods	Provide fish migration and spawning cues
	Provide new feeding opportunities for fish and waterbirds
	Recharge floodplain water table
	Maintain diversity in floodplain forest types through prolonged inundation (plant species have differing tolerances for flooding)
	Control distribution and abundance of plants on floodplain
	Trigger new phases of life cycles (e.g. insects)
	Enable fish to spawn on floodplain, provide nursery area for juvenile fish
	Deposit nutrients on floodplain
	Maintain balance of species in aquatic and riparian communities
	Create sites for recruitment of colonizing plants
	Shape physical habitats of floodplain
	Deposit substrata (gravel, cobble) in spawning areas
	Flush organic materials (food) and woody debris (habitat structures) into channel
	Purge invasive, introduced species from aquatic and riparian communities
	Disburse seeds and fruits of riparian plants
	Drive lateral movement of river channel, forming new habitats (secondary channels, oxbow lakes)
	Provide plant seedlings with prolonged access to soil moisture

Although the various components of the flow regime are most often examined independently in terms of the roles they fulfil, in reality they interact in concert, often synergistically, and in a highly complex manner (Poff *et al.* 1997). High- and low-flow events are considered of particular significance in that they may act as ecological bottlenecks, presenting critical stresses or opportunities for riverine biota (Poff and Ward 1989; Poff *et al.* 1997; O'Keeffe *et al*. 2002). Empirical evidence for the adaptation of riverine biota to such flow extremes, in particular, is provided in Lytle and Poff (2004).

1.4.3 The role and nature of disturbance in rivers

Disturbance (particularly physical) has gained prominence over the years (Fisher and Grimm 1988) as arguably the dominant factor generating the temporal environmental variability and spatial heterogeneity that typify riverine ecosystems (*inter alia*, Stanford and Ward 1983; Sousa 1984; McAuliffe 1983, 1984; Menge and Sutherland 1987; Minshall 1988; Townsend 1989; Menge and Olson 1990; Poff and Ward 1990; Levin 1992; Poff *et al.* 1997; Palmer and Poff 1997; Bunn and Arthington 2002; Naiman *et al*. 2002). Disturbance events are recognised as highly influential in the characterization, organization and constraint of river ecological patterns and processes (Sousa 1984; Pickett and White 1985; Boulton *et al*. 1988; Pickett *et al*. 1989; Resh *et al*. 1988; Fisher and Grimm 1988, 1991; Grimm and Fisher 1989; Niemi *et al*. 1990; Reice *et al.* 1990; Poff and Ward 1990; Stanley and Fisher 1992; Scarsbrook and Townsend 1993; Townsend and Hildrew 1994; Hildrew and Giller 1994; Grimm 1994; Townsend *et al*. 1997a, b).

It has been suggested that the major role of disturbances in rivers may be in reorganising and maintaining spatial and temporal heterogeneity of resources (Section 1.4.5) considered especially critical to maintain the high species richness and rapid energy turnover characteristic of rivers subject to frequent natural disturbances (Brooks and Boulton 1991), rather than in directly impacting faunal abundances (Resh *et al.* 1988; Lake *et al.* 1989). Only fairly recently, however, has the importance of understanding natural variability in rivers been recognized as an appropriate baseline against which to assess the impacts of disturbance and the recovery rates of aquatic communities (e.g. Palmer *et al.* 1997; Palmer and Poff 1997; Boulton 2003). Knowledge remains insufficient (Niemi *et al.* 1993), yet an ability to predict impacts of various disturbances is recognised as highly beneficial for the future of river conservation and management (Minshall 1988; Death 1996a; Bunn and Arthington 2002).

Basis of disturbance theory

As Townsend *et al*. (1997a) commented, the definition of what constitutes a disturbance for riverine communities and the ways to describe its importance are an evolving area of stream ecosystem theory (e.g. Resh *et al*. 1988; Townsend 1989; Wallace 1990; Reice *et al.* 1990; Poff 1992; Townsend and Hildrew 1994; Milner 1994; Collins and Glenn 1997; McCabe and Gotelli 2000). A wide spectrum of population and community-based models have fuelled such theoretical advancement, discussion of which is beyond the intent of this thesis (but for examples see: Ward and Stanford 1983b; Krebs 1985; Minshall and Petersen 1985; Minshall 1988; Resh *et al.* 1988; Townsend 1989; Frid and Townsend 1989; Lake *et al.* 1989; Reice *et al.* 1990; Hildrew and Giller 1994; Townsend and Hildrew 1994; Death and Winterbourn 1995; Wootton 1998; Downes *et al*. 1998a, b).

In early thinking, disturbances to natural systems tended to be viewed as abnormal, uncommon or irregular events that resulted in abrupt structural changes to communities that transformed them from near-equilibrium status (Resh *et al*. 1988; Pickett and White 1985). There has been gradual acceptance in the main that such a view of disturbance is prescriptive and outdated and that physical and biological disturbances are a natural

feature of many environments, where they structure communities and maintain diversity, and where communities may respond predictably to disturbance (Fisher 1983; Pickett and White 1985; Power *et al*. 1988; Poff 1992). Sousa (1984) adopted the view that disturbance was located towards one extreme of the continuum of natural perturbations affecting biota. Disturbance was defined in the context of population dynamics, in terms of the relationship between environmental variability and fitness (Poff 1992; Townsend and Hildrew 1994), as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates and opportunity for new individuals (or colonies) to become established" (Sousa 1984, p. 356). Minshall (1988, p. 277) focused more on the detrimental aspect of disturbance, viewing it as a "destructive, rapid (e.g. spate) or prolonged (e.g. drought) change in the physical environment which exceeds the normal range of conditions experienced by a substantial number of organisms in a population or community or the rate of their ability to adjust, resulting in their death and/or removal."

White and Pickett (1985, p. 7) defined disturbance from a similar, but broader, perspective as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." In this widely accepted definition (Death and Winterbourn 1994) disturbance included natural (environmental fluctuations) or destructive events, might occur along a continuum from exogenous to endogenous events, and was relative to the spatial and temporal dimensions of the system under study. Further, White and Pickett (1985) recognised the role of disturbance in opening up spaces, thereby making available resources and creating 'patchiness', though diffuse disturbance effects might render the patches difficult to delineate (Section 1.4.5). Both Sousa (1984) and White and Pickett (1985) considered disturbances as discrete events, the impact of which could be measured in terms of ecological responses (Poff 1992). Further, they recognised that the statistical distribution of individual disturbance events, on the basis of the historical record, in terms of attributes such as magnitude (intensity), frequency, duration, extent and predictability, is characteristic of a particular disturbance regime. Lake (2000) emphasised that disturbances applied to the habitat space occupied by a population, community or ecosystem should additionally be defined by their potentially damaging, mainly abiotic, properties, particularly the form and intensity of their force.

Niemi *et al*. (1990) and Yount and Niemi (1990, p. 547) broadly adopted White and Pickett's (1985) definition, but considered a disturbance to refer to a situation where one or more stressors result in a change in system state that is different from "nominal behaviour" (a value-free term in place of 'natural' or 'unstressed'). Wallace (1990, p. 605) referred to disturbance specifically in relation to invertebrates as "any event that results in a significant change (either positive or negative) in macroinvertebrate community structure (species, abundance, biomass, or production) beyond that expected over the annual cycle within a particular habitat." In contrast, Townsend (1989), Townsend and Hildrew (1994), Hildrew and Giller (1994) and Townsend *et al*. (1997a) did not attempt to differentiate between normal or abnormal disturbances, as characteristic features of rivers. Rather, like several other authors above, they adopted a patch dynamics

perspective (Section 1.4.5), considering disturbance as "any relatively discrete event that removes organisms and opens up space or other resources that can be used by individuals of the same or different species" (Townsend *et al*. 1997a, p. 531).

Resh *et al.* (1988) amended White and Pickett's (1985) concept of disturbance, to encompass only events outside a predictable range of environmental variability, but acknowledged this merited scrutiny. Predictability, though difficult to characterise, was considered an attribute of central importance in that certain events might represent regular endogenous features of the riverine ecosystem to which the biota would be expected to be adapted (e.g. seasonal discharge or temperature fluctuations, but cf. Poff 1992) rather than unnatural or anthropogenic disturbance events outside a predictable range. Resh *et al.* (1988, p. 433) therefore defined disturbance as "any relatively discrete event in time that is characterized by a frequency, intensity, and severity outside a predictable range, and that disrupts ecosystem, community, or population structure and changes resources or the physical environment".

Poff (1992), Uys and O'Keeffe (1997a) and others challenged Resh *et al*.'s (1988) assertion that disturbances are unpredictable, particularly because it did not make the explicit, critical distinction between ecological and evolutionary time scales of biotic response to disturbance, or allow for predictability to be examined as a separate component of the disturbance regime. Death and Winterbourn (1994, p. 126) endorsed Poff's (1992) view, observing that "environmental stability is related to changes in the environment, irrespective of the predictability of those changes". Poff (1992, p. 86) stated that "disturbances (including predictable ones) always have ecological effects; however, the magnitude of ecological response to a particular disturbance may be constrained by evolutionary (historical) adjustments of the biota if the disturbance regime is characterized by high predictability." Thus, if the temporal distribution of a perturbation is 'sufficiently predictable', ecological responses may be limited inasmuch as organisms and communities have adjusted to them in the long-term. If the environmental selection regime comprises extreme events that are (1) frequent in occurrence (relative to the lifespan of the organism), (2) contingent (predictable), and (3) not too deviant (relative to normal conditions), then adaptation by an organism is feasible, though different combinations of these properties would influence whether or not adaptation would be favoured and in what form (Thiery 1982, cited in Poff 1992). Hence, Poff (1992, p. 89) argued that "potential adaptation to disturbance predictability is itself contingent upon other attributes of the disturbance regime", and that rather than assuming a level of adaptation to predictable events, it would be more effective to explore the extent to which organismal or ecosystem attributes vary among streams depending on the "predictability or various interactive components of the disturbance regime". It was noted too that "Differences within or among streams with respect to ecological responses to specified disturbance intensities can be *hypothesized* to reflect differences in disturbance regimes (predictability, frequency) among sites, but data are needed to test such hypotheses" (Poff 1992, p. 91).

Resh *et al.* (1988) focused on quantification of the characteristics of the disturbance event (e.g. a flood) rather than of the response (e.g. a flow induced change in invertebrate assemblage composition). Such a distinction between the characterisation of disturbance in terms of its principally abiotic 'input properties' (*sensu* Lake 2000) rather than, as done by Sousa (1984) and White and Pickett (1985), on the basis of the effects on the biota and subsequent biotic responses, is increasingly endorsed. According to Lake (2000), by not characterising a disturbance in terms of its outcome or biotic effects it is possible to develop more standardised ways of comparing impacts of the same disturbance type in different systems, or different types of disturbance in the same system. Lake (2000, 2003), following Bender *et al*. (1984), Glasby and Underwood (1996) and others, recognised that an ecological perturbation comprises two sequential events, the first being the disturbance (or cause, marked by the application of some disturbing force) and the second the response shown by the biota (the effect). Poff (1992) advocated the use of physically based measures of flow disturbance (e.g. the discharge at which substratum mobilisation is initiated) for which specific ecological responses can be determined, in lieu of the statistical criteria suggested by Resh *et al*. (1988). Other researchers have also recognised that "a physically based measure of disturbance relates more directly to the organism" (Scarsbrook and Townsend 1993, p. 396) and does not place the same limitations as purely statistical hydrologic criteria on characterisation of the disturbance regime.

For the purposes of this thesis, and specifically in relation to flow variability (see below), a broad view of disturbance is adopted along the lines of Poff (1992), Townsend *et al*. (1997a) and Lake (2000). The distinction advocated by Lake (2000, 2003) and others was made between the characteristics of the low flow event as the physical disturbance and the nature of the abiotic and/or biotic responses observed, so that comparisons were possible among multiple rivers in time and space (Resh *et al*. 1988; Poff and Ward 1989; Section 1.2 and Chapter 3).

Disturbance gradients

Over the past decades, there has been much debate among ecologists regarding the placement of lotic communities along a generalized disturbance axis, grading from highly unpredictable environments largely influenced by physical processes, to more constant or regularly fluctuating, low disturbance environments with more stable communities (Peckarsky 1983; McAuliffe 1984; Reice 1985; Minshall and Petersen 1985; Menge and Sutherland 1987; Minshall 1988; Townsend 1989; Power *et al*. 1988; Reice *et al*. 1990; Death and Winterbourn 1994). The view is generally held in this harsh-benign conceptual model of community structure (Peckarsky 1983) that biological interactions (e.g. predation, competition) are intimately linked to abiotic variation (Power *et al*. 1988) and assume less importance, or play a subordinate role, as determinants of community structure as abiotic disturbances (most notably flow regime) increase (Peckarsky 1983; Ward and Stanford 1983b; Fisher 1983; McAuliffe 1984; Minshall and Petersen 1985; Boulton and Suter 1986; Hildrew and Townsend 1987; Fisher and Grimm 1988; Poff and Ward 1989; Lancaster *et al*. 1990; Poff and Allan 1995).

Based on empirical evidence, lotic communities are thought to tend towards control by abiotic factors, particularly in rivers exhibiting highly variable hydrological regimes and dynamic habitats (e.g. Townsend 1989; Townsend and Hildrew 1994). A premise underlying Poff and Ward's (1989) flow-regime based model of river classification is that abiotic processes predominate in importance in controlling lotic ecological processes and patterns in situations where flow regimes are highly variable and/or unpredictable, while more predictable and less disturbed flow environments enable biotic interactions to be more influential. For the majority of rivers, it is recognised that their hydrological regimes fall between disturbance extremes, such that both abiotic and biotic factors contribute to community structure at different times and at different scales (McAuliffe 1984; Minshall 1988; Power *et al.* 1988; Menge and Sutherland 1987; Southwood 1988; Uys and O'Keeffe 1997b). Despite some lack of consensus among stream ecologists as to whether flow regime variability/predictability, and hence disturbance regime, regulate the extent to which abiotic or biotic factors are more important determinants of community structure, explanatory power is considered greater if the interactions of both factors are considered (Dudgeon 1993). Moreover, although the emphasis in river research is on the role of physical flow-related disturbance (see below), it is generally acknowledged that there is also a need to consider biotic interactions in relation to disturbance or as disturbances in themselves (e.g. McAuliffe 1983), especially under potentially stressful conditions such as might be expected to occur at flow extremes.

Types of disturbance

Disturbance events may be allogenic (imposed from outside the system) or autogenic (generated by processes within it), and are often superimposed and/or interactive (Fisher and Grimm 1991; Grimm 1994). Allogenic disturbances tend to be abiotic, occurring at larger spatiotemporal scales than autogenic ones, with floods and drying events cited as examples (Grimm 1994). Autogenic events, in contrast, are usually biotic and small-scale (e.g. invertebrate grazing).

Three broad types of disturbances may be recognised, namely *pulse*, *press* (Bender *et al.* 1984; Glasby and Underwood 1996) and more recently *ramp* disturbances (Lake 2000, Figure 1, p. 575; see Section 3.1 for the disturbance type examined in this study). Models simulating press and pulse disturbances had different outcomes, as did studies of recovery from different disturbance types and their timing, suggesting that differences among disturbance types may be pertinent in developing relationships between disturbance and response (Bender *et al.* 1984; Niemi *et al*. 1990; Yount and Niemi 1990; Boulton 2003). Bender *et al.* (1984) described a pulse disturbance as an event of typically limited and readily definable duration, such as a flood or low flow event, and went on to link it to a response where a given population was instantaneously reduced and subsequently recovered (while Lake (2000), addressed the nature of the disturbance and the response separately). Pulse disturbances are of short duration, relative to the generation times of longer-lived susceptible species, and frequently localised, so that recovery is likely to be from nearby undisturbed areas or internal refugia (Yount and Niemi 1990; see discussion on recovery below). Recovery also tends to be rapid, as long as recolonisation sources are accessible (Minshall and Petersen 1985) and the disturbance is confined

(Yount and Niemi 1990). A press disturbance is a prolonged disturbance, where a species is permanently removed (Bender *et al.* 1984), and which may commence sharply and then maintain a constant level (Lake 2000). Such disturbances are typically the result of anthropogenic activities and often involve changes in the catchment or stream channel (Niemi *et al*. 1990; Lake 2000). According to Lake (2000, 2003), 'ramps' occur when the strength of a disturbance steadily increases (or decreases) over time, often simultaneously increasing spatially, either without an endpoint or levelling off to an asymptote after an extended time period (e.g. persistent supra-seasonal drought). The trajectory of response to a disturbance event might take one of the same three forms - pulse, press or ramp - with, for instance, a pulse disturbance producing a press or pulse response (Glasby and Underwood 1996; Lake 2000, p. 576, Figure 2).

It may be especially difficult to distinguish low-level anthropogenic perturbations from normal variations imposed by long-term natural cycles (Schindler 1987). Moreover, even natural, non-novel phenomena (e.g. low flows) have the potential to constitute a disturbance once biotic tolerance levels are exceeded (Poff and Ward 1990; Boulton 2003). Brooks and Boulton (1991) highlighted too the difficulty with episodic events of determining the beginning and end of the disturbance.

Disturbance regime descriptors

Operational definition and quantification of descriptors of a river disturbance regime, at spatial and temporal scales appropriate to enable detection of disturbance effects on any given biological response variable or recovery (Fisher *et al.* 1982; Poff and Ward 1990; Reice *et al.* 1990; Levin 1992; Scarsbrook and Townsend 1993; Townsend and Hildrew 1994; Townsend *et al*. 1997a), though complex is essential to progress meaningful comparisons among disturbance events and systems (Lake 2000). Moreover, the disturbance measure(s) should necessarily be of clear relevance to the organisms concerned (Poff and Allan 1995; Townsend *et al*. 1997a).

Given the hierarchical, scale-dependent nature of disturbance, with a physical event constituting a disturbance at one level, but not at another, the scale at which disturbance is examined is liable to alter perceptions of the main controlling factors involved (Harris 1980; Levin *et al*. 1984; Frissell *et al.* 1986; Minshall 1988; Statzner *et al.* 1988; Levin 1992; Boulton *et al.* 1992a; Wu and Loucks 1995; Cooper *et al.* 1997) and should be guided by the ecological question of interest (Poff 1992). Both the scale over which the disturbance acts, and the scale at which the biota respond, are pertinent (Downes *et al*. 1998a). As spatial scale increases from small to large, the frequencies of temporal phenomena tend to decrease, affecting the continuum in levels of ecological organisation and response characteristics, from those pertaining to the individual to those of the community or whole ecosystem (Poff and Ward 1990). The way in which variance changes with spatial or temporal scale may also generate new, biologically meaningful insights (Palmer *et al*. 1997, p. 191, Figure 1; Palmer and Poff 1997). River ecologists have tended to rely on disturbance measures derived predominantly from hydrological and geomorphological thinking (e.g. Newbury 1984), according to

Townsend *et al*. (1997a), where the scale at which the measures were developed might not be of direct relevance for addressing ecological questions.

Sousa (1984) and Pickett and White (1985) identified various descriptors for the characterization of a disturbance regime in space and time (Table 1.4). Studies of the role of disturbance in rivers have evolved over time from straightforward descriptions of discrete phenomena to attempts to rigorously test specific hypotheses on the ecological roles played by disturbance. While a range of approaches have been developed to measure aspects of the disturbance regime using such descriptors, limited attention has been directed at assessing their actual suitability for testing specific hypotheses (Townsend *et al*. 1997a; Palmer and Poff 1997).

Table 1.4 Definitions of disturbance regime descriptors (adapted from Sousa 1984; Pickett and White 1985). For a given disturbance descriptor, measures of central tendency and dispersion, as well as frequency distributions, are of interest.

DESCRIPTOR	DEFINITION
Distribution	Spatial distribution, including relationship to geographic, topographic, environmental, and community gradients.
Frequency	Mean number of events per time period. Frequency is often used for probability of disturbance when expressed as a decimal fraction of events per year.
random point	Mean number of disturbances per unit time at a random point within a region. Often expressed as recurrence or return interval (i.e. the average time between disturbances).
regional	The total number of disturbances that occur in a geographical area per unit time.
Return interval, cycle or turnover time	The inverse of frequency; mean time between disturbances.
Rotation period	Mean time needed to disturb an area equivalent to the study area (the study area is arbitrarily defined; some sites may be disturbed several times in this period and others not at all - thus, "study area" must be explicitly defined). Equivalent to turnover rate.
Predictability	A scaled inverse function of variance in the return interval (i.e. the variance in the mean time between disturbances).
Area or size	Area disturbed. This can be expressed as area disturbed per event, area per time period, area per event per time period, or total area per disturbance type per time period. Frequently given as a percentage of total available area. Fraction of habitat affected/areal extent is considered by some authors (e.g. Scarsbrook and Townsend; Hildrew and Giller 1994; cf. intensity as defined below) to reflect disturbance intensity.
Magnitude	
intensity	Physical force or strength of the event per area per time (e.g., heat released per area per time period for fire).
severity	Damage or impact caused by the disturbing force on the organism, community, or ecosystem (e.g., basal area removed).
Synergism	Effects on the occurrence of other disturbances (e.g., drought increases fire intensity).

The degree of disturbance experienced and the resultant response have been shown to be influenced by factors such as the area affected, and the intensity, magnitude, duration, frequency and mechanisms of the disturbance event (Townsend 1989; Poff and Ward 1990; Boulton *et al.* 1992a; Townsend *et al*. 1997a; Downes *et al*. 1998a; Wootton 1998). The size of the disturbed area/patches relative to the size of the system is considered perhaps the most important spatial criterion, affecting the rate and dynamics of the recovery process (Fisher 1987; Minshall 1988; see below). Wallace (1990) also pointed out that recovery times may be as much related to river size as to disturbance type. Where the extent of the disturbed area is small,

recolonisation has been shown to be rapid, due to the close proximity of colonists in the surrounding river bed (Brooks and Boulton 1991). Where disturbance affects localised patches as opposed to a complete river reach or section, recolonisation can be viewed more appropriately as a redistribution of the benthos (Matthaei *et al*. 2000; this thesis – Chapter 7), rather than colonisation after a catastrophic event (e.g. Fisher *et al.* 1982).

Disturbance magnitude, intensity and frequency also have been demonstrated to influence recolonisation of the disturbed area and species composition following recovery (Pickett and White 1985; Boulton *et al*. 1988; Reice *et al*. 1990; Sedell *et al*. 1990; Lancaster and Hildrew 1993a; Townsend and Hildrew 1994); disturbance intensity and frequency may be treated synonymously (e.g. Lake *et al.* 1989). Larger-scale, infrequent disturbances may result in qualitatively different responses from disturbances of higher frequency, and concomitantly typically lower intensity, which affect a small proportion of the habitat (Hildrew and Giller 1994; Naiman and Turner 2000). Severe disturbances of short duration may be less impactful than longer duration disturbances of moderate impact (Niemi *et al*. 1993). Disturbance frequency has been studied in two main ways, in terms of how it is thought to affect the biota (Death 1996b), as either changes in event frequency *per se* (i.e. the number of disturbances a patch experiences; e.g. Doeg *et al*. 1989; Lake *et al*. 1989) or in terms of time for colonisation since the last disturbance event (e.g. Death 1996b). Death and Winterbourn (1995) considered the latter factor to be more important in determining species richness.

Understanding remains inadequate of whether increases in the intensity or frequency of disturbance exert similar effects on riverine biota, and of the possible interaction effects of the two disturbance factors (e.g. in terms of area affected) (Death and Winterbourn 1995). Grimm and Fisher (1989) speculated that in terms of disturbance regime, disturbance magnitude may be most closely connected to resistance, while timing and frequency might exert a greater influence on resilience as they dictate the time available for recovery. As the magnitudes of disturbance measures such as frequency and intensity increase, the degree of patchiness (Section 1.4.6) and the relative importance of colonising ability and mobility over biotic factors (e.g. competitive ability) are expected to increase (Scarsbrook and Townsend 1993). Reice *et al*. (1990) postulated that the magnitude of response in populations might be directly proportional to disturbance frequency, and suggested that benthic communities that are most frequently and predictably disturbed may be best adapted to disturbance and most resilient (Section 1.4.3).

Disturbance history

Poff and Ward (1990, p. 638) noted that there is a "history-dependent framework", with biotic response to disturbance likely to vary substantially among different rivers on the basis of historical patterns of natural variability and disturbance. Several authors, among them Poff and Ward (1990), Reice *et al*. (1990) and Townsend and Hildrew (1994) consider biotic response to disturbance, including resistance to and recovery from it, to be a function of the long-term spatial and temporal patterns of variation experienced by the biota (i.e. the different habitat templates to which the biota have become accustomed - Section 1.4.5).

Importantly, Poff and Ward (1990, p. 629) considered that "the spatial and temporal characteristics of the physical environment may predetermine the type and range of ecological response mechanisms available following natural and anthropogenic disturbances." Furthermore, community complexity has been hypothesised to be a result of disturbance history, and has been related to a community's ability to cope with disturbance (Death 1996b). There remain few studies, however, that have explicitly investigated, particularly experimentally (but see Mackay 1992), whether or not the disturbance history of an invertebrate community affects that community's ability to respond to a disturbance (Death 1996b). The potential importance of low-flow disturbance history was addressed in this thesis (Chapter 4).

The life history approaches adopted by invertebrate species and the pattern of strategies of the entire assemblage, including behavioural, physiological and reproductive responses, are considered to vary according to the predictability, type, frequency and intensity of the disturbance (Resh *et al*. 1988; Townsend 1989; Townsend and Hildrew 1994). Moreover, the extent to which a particular physical event acts as a disturbance may be in part a function of its scale relative to the size and generation time of the organism(s) concerned (Townsend and Hildrew 1994).

Several studies have demonstrated the importance of having an understanding of the pre-disturbance community and potential sources of colonists, in addition to the spatial and temporal scales of the event itself (e.g. Fisher *et al.* 1982; Townsend 1989; Peterson and Stevenson 1992). Contemporary theory and disturbance studies suggest that lotic populations and assemblages from more naturally variable, disturbed systems should possess greater resistance and persistence (*sensu* Connell and Sousa 1983), and thus, respond less markedly and/or recover faster than those of more constant environments to disturbances (Poff and Ward 1990; Milner 1994). Disturbances have been reported to strengthen the pattern of preponderance of resistance or resilience traits of riverine insects, with taxa associated with more disturbed conditions generally displaying a larger number of such traits, combined, than taxa associated with more stable stream environments (e.g. Townsend *et al*. 1997b). The response of a river assemblage to disturbance and its ability to recover are expected to be related in part to the structural (taxonomic) and functional diversity of its individuals (Resh *et al*. 1988); species richness and density, for example, constitute useful measures of degree of recovery. As some species may be more susceptible to disturbance than others (Sousa 1984; but see, for example, Doeg *et al*. 1989), disturbances will usually leave a relict fauna (*sensu* Townsend 1989), a subset of the original fauna that may influence subsequent recovery (Frid and Townsend 1989). Importantly, a quantitative study of flood disturbance by Townsend *et al*. (1997a, p. 541) highlighted the point that "the most appropriate measure of disturbance may vary even among quite closely related taxa".

Biotic response to disturbance - resistance and resilience

Ecosystem stability has proved conceptually useful for understanding biotic response to disturbance (Holling 1973; Harrison 1979; Connell and Sousa 1983; Webster *et al.* 1983; Wu and Loucks 1995), which can be subdivided into two main components, resistance and resilience. These two components are the result of a

complex set of underlying mechanisms (Peterson and Stevenson 1992; Milner 1994; see below) and provide a means of quantifying the effects of a disturbance on a given state variable (Grimm and Fisher 1989; Stanley and Fisher 1992). Stability and the persistence of communities subjected to disturbance may be attained if state variables exhibit some combination of the attributes of resistance and resilience (Boulton and Suter 1986; Townsend *et al.* 1987; Minshall 1988; Grimm and Fisher 1989; Doeg *et al*. 1989; Fisher and Grimm 1991; Brooks and Boulton 1991; Stanley and Fisher 1992; Boulton *et al.* 1992b; Milner 1994; Death and Winterbourn 1994, 1995; Townsend and Hildrew 1994; Death 1996a, b).

Resistance is measured as "the capacity to withstand the disturbance without appreciable loss of individuals" (Harrison 1979; Townsend *et al*. 1997a, p. 368), or to initially resist or be unaffected by it. It may be reflected as the extent to which a disturbance changes the system, such as the percentage change in population measures (Fisher and Grimm 1988, 1991; Stanley and Fisher 1992; Townsend and Hildrew 1994; Milner 1994). The absence of a temporal component to the definition implies that the disturbance event is instantaneous, an assumption that accords with many (but not all) disturbance definitions in which the event is punctuated (Sousa 1984) or a short pulse (Stanley and Fisher 1992). Resistance to disturbance has been found to be dependent on several factors, including: disturbance magnitude (Sousa 1980; Grimm and Fisher 1989); aspects of pre-disturbance history, such as harshness or stability of habitat (Gurtz and Wallace 1984) or assemblage successional age (Sousa 1980); life history characteristics, life stage and growth form of the biota. For most types of disturbance, there is likely to be a threshold of disturbance intensity above which aquatic biota are not resistant (Grimm and Fisher 1989; Fisher and Grimm 1991).

The second component of disturbance response is resilience, "the capacity for a rapid return towards the density prevailing before the disturbance" (Townsend *et al*. 1997a, p. 368) or some other reference state following displacement by disturbance (Wallace 1990), represented by the slope of the recovery trajectory (Death 1996b). A resilient species population would exhibit rapid recovery after a disturbance (see Stanley and Fisher 1992, p. 274, Figure 2; Fisher and Grimm 1988; Yount and Niemi 1990; Townsend and Hildrew 1994; Townsend *et al*. 1997a). Peterson and Stevenson (1992) in a study of resistance and resilience of lotic algal communities to flow disturbance observed that the most appropriate measure of resilience was convergence with a temporally changing, undisturbed control community, rather than simply a return to a pre-disturbance state (a view adopted in this thesis; Chapter 7). A key aspect of resilience, succession is simply used to reflect the sequence of changes in community composition at a site post-disturbance (Grimm and Fisher 1989; Fisher 1990; Boulton and Lake 1992a, b). The basis for resilience resides in both the physical environment providing refugia (Section 1.4.4) and in organism characteristics (Hildrew and Giller 1994).

Measuring recovery

Niemi *et al.* (1993, p. 1542, and p. 1543, Figure 1) provided a useful, measurable definition of recovery as "the time (t) in which a response variable is no longer significantly different ($p < 0.05$) between comparable

measurements gathered before and after a disturbance" - assuming that a response variable significantly changed following exposure to the disturbance or stress (this definition was adopted for the assessment of invertebrate recovery from flow reduction; Chapter 7). Poff and Ward (1990) noted that the duration of the recovery phase is dependent on the recovery mechanisms or ecological processes involved, as well as the extent to which the biota are pre-adapted to deal with the particular form of disturbance. Although a particular stressor may result in a more marked impact in one aquatic system than another, leading to the conclusion that the stressor in the former system is more detrimental, recovery may be far slower to non-existent in the less substantially altered system and thus, reflect a more serious impact in the longer-term (Niemi *et al*. 1990, p. 572, Figure 1).

Multiple factors, including disturbance type and the importance of a variable for ecosystem condition, have influenced the choice of variables for measuring recovery from disturbance (Milner 1994; Niemi *et al.* 1993). The lack of data on responses to disturbance and recovery rates, as well as the absence of pre-disturbance data to properly assess whether or not a river system has recovered from disturbance, remain impediments to the identification of appropriate variables (Niemi *et al.* 1993). Many of the over 150 North American case studies (79% lotic, mostly small to medium-sized systems) of the recovery of freshwater ecosystems from various forms of disturbance assessed by Niemi *et al.* (1990) were limited in scope, and few were designed specifically to examine recovery (Niemi *et al.* 1993). Recovery has been most commonly measured by factors such as the first reappearance of a species, return time of pre-disturbance densities or average individual size, recovery of species richness or of total biomass (Niemi *et al.* 1990).

Factors influencing recovery rate and pathways

A variety of factors are known to contribute to the inherent ability of a river to recover from (flow-related) disturbance and the rate of recovery of reduced or impacted populations of different organisms, principal among them life history characteristics of individual taxa and system physical characteristics (Power *et al*. 1988; Minshall 1988; Statzner *et al.* 1988; Yount and Niemi 1990; Niemi *et al.* 1990; Wallace 1990; Brooks and Boulton 1991; Lancaster and Hildrew 1993a; Milner 1994; Townsend and Hildrew 1994; Matthaei *et al*. 1997; Lake 2000). Factors reported in the literature have included: disturbance type; persistence of the impact; time of year in which the disturbance occurs; availability of suitable refugia; and life history traits and other biological attributes of the community (e.g. physicochemical tolerances, life span, generation time, emergence times, fecundity, timing of reproduction and other life cycle activities relative to disturbance timing, mobility/dispersal capabilities, population growth rates, species body size, competition-predation interactions among resident species).

In the case of habitat patch disturbance, additional related factors have been found to influence invertebrate recovery, including the effectiveness of the redistribution or recolonisation process, the distance to or degree of isolation from an (undisturbed) recolonisation source (and in an upstream or downstream direction), the ratio of edge to interior of disturbed patches, active or passive movement into the refugium, effectiveness of

retention of organisms, and the proportion of the population that can be accommodated (e.g. Sedell *et al.* 1990; Reice *et al*. 1990; Milner 1994; Townsend and Hildrew 1994; Hildrew and Giller 1994; Matthaei *et al*. 1997). Where the disturbed area was located far from refugia or a residual population did not persist, life history characteristics and adult mobility assumed greater importance in dictating recovery rate (Niemi *et al*. 1990; Lancaster and Hildrew 1993a; Scarsbrook and Townsend 1993).

Studies have suggested that while riverine biota tend to exhibit low resistance to disturbance (notably below the reach scale) resilience, particularly at small patch scales, tends to be high (e.g. Townsend and Hildrew 1976; Reice 1985; Minshall and Petersen 1985; Doeg *et al.* 1989; Death 1996b; Lake 2000). While Power *et al*. (1988) observed that for discharge-related disturbance specifically, for most species information was insufficient to evaluate the relative importance of resistance and resilience in recovery, some studies have shown otherwise (e.g. Boulton and Lake 1992a, b; Miller and Golladay 1996). As might be anticipated, recovery generally was more rapid from pulse than from press disturbances (Niemi *et al*. 1990; Lake 2000), as well as with smaller-scale and/or lower intensity disturbances (Townsend 1989). Significantly, Yount and Niemi (1990, p. 563) observed that "anthropogenic disturbances that mimic or produce biotic responses similar to natural disturbances will likely follow similar recovery scenarios." Recovery times tended to be less than three years, and frequently less than a year, except in cases where disturbance resulted in physical alteration of existing habitat, the system was isolated and recolonisation was suppressed, or where residual pollutants persisted (Niemi *et al.* 1990; Yount and Niemi 1990). Niemi *et al*. (1990) and Milner (1994) found that 85% of macroinvertebrate recovery endpoints to pre-disturbance density following pulse disturbances (including floods and low flow events) occurred within 18 months if physical habitat diversity was unaltered. Recovery was within one year for more than 90% of post-disturbance observations of invertebrate total density, total biomass and taxon richness, with no consistent differences in rate among these measures (Niemi *et al.* 1990). Brooks and Boulton (1991) classified taxa according to recolonisation rate during an experimental disturbance reproducing a flood, but the same classification might well be appropriate for low flows: 'fast' recolonisers attained pre-disturbance densities within 1-2 days in all three substrata examined; taxa with 'moderate' recolonisation rates achieved pre-disturbance densities in at least two of the three substrata within four days; and all remaining taxa were categorised as 'slow' colonisers.

Most commonly cited reasons for the typically short recovery times observed for invertebrates were (Yount and Niemi 1990): the fact that lotic systems are naturally subjected to a wide range of disturbances, in response to which the biota have evolved life cycle characteristics that favour adaptability or flexibility, and that promote rapid repopulation of impacted areas; the availability and accessibility of internal refugia (in the majority of instances, rapid recovery rates indicated survival of some individuals in refuges; Section 1.4.4), and unaffected upstream and downstream areas, as sources of organisms for repopulation; and high flushing rates that allowed rapid replacement or dilution of poor quality water.

Niemi *et al.* (1990) reported that total invertebrate density typically recovered more rapidly than most individual taxa, a result attributed to a proliferation of taxa with short generation times (usually dipterans, such as chironomids and simuliids) with elimination of competitors and predators; some multivoltine taxa (e.g. some Diptera and Ephemeroptera) may pass from egg through to adult in less than two weeks in warmwater streams (e.g. Gray and Fisher 1981). Niemi *et al.* (1990, p. 578, Table 6) summarized the range of recovery times for different macroinvertebrate groups, ranking time to recovery for major orders as follows: Diptera < Ephemeroptera < Trichoptera < Plecoptera; Coleopterans recovered at a similar rate or more slowly than Trichoptera and Plecoptera. Ephemeroptera and Diptera, for example, possess a wide range of life histories (so non-sensitive resting or aestivating life stages, or reproductive adults, are more likely to be present after unpredictable disturbances), as well as high drift rates relative to benthic standing crop (Townsend and Hildrew 1976; Brittain and Eikland 1988). Trichopterans showed slower recovery rates, because they have less variation in life history features, may have generation times greater than a year, and are often attached or sessile, reducing the tendency to drift (Niemi *et al.* 1990).

Five main avenues of redistribution or recolonisation exist from flow-related disturbance, for benthic invertebrates (Townsend and Hildrew 1976; Williams and Hynes 1976; Corkum *et al.* 1977; Minshall and Petersen 1985; Brittain and Eikland 1988; Wallace 1990; Crisp 1995; Lake 2000): (1) downstream migration, notably by drift - a natural dynamic process of downstream transport of aquatic organisms in the current under both high and low flow regimes, with a continual loss of some organisms from the substratum and settling out of others; (2) upstream migration, though movements along the bottom; (3) aerial migration (either by oviposition or adults); (4) vertical migration of individuals from within the deeper hyporheic zone (subsurface refugia) to surface substrata; and (5) hatching or reactivation of drought-resistant stages.

Downstream drift has been identified as the primary redistribution mechanism, particularly for small habitat patches (Williams and Hynes 1976; Townsend and Hildrew 1976; Minshall and Petersen 1985; Brittain and Eikland 1988; Doeg *et al.* 1989; Townsend 1989; Niemi *et al*. 1990; Wallace 1990). Different species exhibit varying abilities to drift and redistribute depending on biological and physical conditions. As only a very small fraction of the biota are in the drift at any one time, and typically for a limited period (Brittain and Eikland 1988), the riverbed remains the focus for processes structuring communities (Minshall and Petersen 1985). Though several recovery routes are liable to be similar for high and low flow events, reduced discharge places a limit on effective drift in the water column (Lake 2003; James *et al*. 2008).

Refugia from disturbance

Particular disturbances are liable to influence habitat patches differentially, as a function of spatial heterogeneity, generating potential refugia for affected organisms (Townsend and Hildrew 1994). Refugia may be broadly defined as "places (or times) where the negative effects of disturbance are lower than in the surrounding area (or time)" (Lancaster and Belyea 1997, p. 222). They play a critical role as buffers against (flow-related) disturbance and as recolonisation sources (Poff and Ward 1990; Townsend 1989; Sedell *et al*.

1990; Hildrew and Giller 1994; Townsend and Hildrew 1994; Lancaster and Belyea 1997; Lake 2000, 2003). Lancaster and Belyea (1997, p. 221) stated that "macroinvertebrates may accumulate in refugia during disturbance events and redistribute throughout the stream after the disturbance". The re-establishment of populations in previously disturbed patches may be a result of rapid reproduction of populations that survived the disturbance in such refugia and/or it could simply stem from movement of surviving individuals back into those patches (Townsend and Hildrew 1994).

Increasing attention has been given by ecologists to the ways in which the differential survival of individuals inhabiting different habitat patches, coupled with the mechanisms for dispersal and refugium use, may explain assemblage recovery from flow-related disturbance (Pringle *et al*. 1988; Sedell *et al*. 1990; Palmer *et al*. 1992). Though both low-flow (drought) and flood refugia are recognised, characterization of the former is less advanced and more remains to be learnt regarding the influence of the patchiness of different refugia on patterns of invertebrate recovery following flow reduction (Lancaster and Hildrew 1993a, b; Lancaster 2000; Lake 2000, 2003).

The heterogeneity and patchiness of the flow itself as reflected in hydraulic variability with changing flow conditions, is recognised as one of the most widely explored classes of flow-related refuges from disturbance (Hildrew and Giller 1994). Although Lancaster and Hildrew (1993a, p. 385) defined flow refugia specifically in relation to floods, as "places not subject to raised hydraulic stress during spates and where density-independent losses of benthic animals are, therefore, likely to be slight", the concept applies equally well to places of low hydraulic or otherwise flow-related stress at very low flows (as in this thesis). Flow refugia may be considered either as temporal synchronies between flow heterogeneity and the life cycle, life history or habitude of an organism, or spatial locations that are not subject to severe hydraulic stress, reducing disturbance-induced population losses (Lancaster and Hildrew 1993a, b; Lancaster and Belyea 1997). Such patches may represent only a small fraction of the total surface area of the river bed (Palmer *et al*. 1992), particularly as the areal extent of the disturbance increases (Scarsbrook and Townsend 1993).

Townsend and Hildrew (1994) identified two main scales at which physical heterogeneity may provide refugia for individuals, namely at the inter-habitat scale ('macroscale refugia') and at the intra-habitat level ('meso-' or 'micro-scale refugia'). As not all areas of habitat of a particular type may be affected by a disturbance, there is the potential for patch recolonisation via migrations of individuals from unaffected places, the macroscale refugia. Alternatively, patchiness within a habitat (e.g. due to variations in hydraulic factors, such velocity or turbulence; Chapter 6) can provide refugia at meso- to micro-scales (Lancaster *et al*. 1990; Townsend and Hildrew 1994; Lancaster and Belyea 1997). The contribution of such refugia to population resilience may depend on the following factors (Townsend and Hildrew 1994): the ability of individuals to actively or passively recolonise the disturbed area and re-establish high densities; the effectiveness with which individuals can move into refugia or are retained in refugia that are already

occupied; and the proportion of the population that is or can be accommodated in a particular refuge (i.e. the total area of refuge available relative to the area disturbed).

At ecological (i.e. outside evolutionary and biogeographic) scales, Lancaster and Belyea (1997, p. 224, Figure 1) identified a hierarchical framework of four scale-dependent classes, of mechanisms of active or passive refugium use by instream biota subject to disturbance. At larger scales (> 1 generation and > 1 habitat patch), where individuals may die as a result of disturbance and external recruitment is required for population persistence, two classes are represented: (1) 'refugia through complex life cycles', through exploiting temporal refugia if different life phases are present simultaneously and for prolonged periods; (2) 'between-habitat refugia', by exploiting more than one habitat patch of similar type (e.g. where parts of a river system are affected unequally). At smaller scales (< 1 generation and ≤ 1 habitat patch), the emphasis is on avoiding or reducing population loss, with individuals surviving disturbance and external recruitment less important. The classes at this scale are: (3) 'refugia through changes in habitude', where biota change their habitat use in order to survive disturbance (e.g. ontogenic shifts in use of microhabitat types, or a change in behaviour within a single patch); and (4) 'within-habitat refugia' where small-scale and short-term spatial and temporal heterogeneity exist among microhabitat patches within a habitat patch (i.e. the effect on patches of different types is unequal, so there exist areas of lesser disturbance). Although high flow examples were used, strategies would be similarly appropriate for low flows (Lancaster and Belyea 1997; Lake 2003).

Conceptual models for class (4), within-habitat refugium use (the most commonly studied; Lake 2000), are detailed by Lancaster and Belyea (1997, p. 227, Figure 2; see Chapter 7, for relevance in the context of this study). In model (A) 'no within-habitat refugia', the habitat patch is homogeneous and a constant proportion of the population is lost at each disturbance, while in (B) 'no flux between microhabitats', population losses occur in all microhabitat types during disturbances, except refugia. Model (C) 'undirected flux', is as for (B), but where individuals subsequently disperse from refugia to other microhabitat types when conditions are more benign. In model (D) 'directed flux', individuals in potentially erosive (or in the case of low flows, for example, potentially desiccated) microhabitats accumulate in refugia (actively or passively), thereby reducing population losses, and with some redistribution of individuals from refugia to other microhabitat types when conditions are more favourable.

1.4.4 Flow as a form of physical disturbance

With the growing appreciation of the ecological importance of physical disturbance in recent years (Section 1.4.3) flow variability, as an obvious source of such disturbance, has attracted the greatest attention (Doeg *et al.* 1989). Considerable interest has been stimulated in assessing the contribution of hydrological patterns to river structure and functioning (Poff and Allan 1995), to the extent that nowadays the hydrological regime is considered probably the most significant disturbance factor influencing riverine ecosystems (Resh *et al.* 1988; Minshall 1988; Power *et al*. 1988; Townsend 1989; Ward 1989; Lake *et al.* 1989; Poff and Ward

1989; Lancaster and Hildrew 1993a; Hildrew and Giller 1994; Puckridge *et al.* 1998; Sections 1.3 and 1.4). Resh *et al*. (1988, p. 443) stated that "until recently, ecological research has seldom been placed in a context that considers past hydrologic conditions or other disturbances" and that "although recent events may dominate observed patterns, the long-term record of extreme flows imposes constraints of an evolutionary nature on the biota." Riverine biota exhibit life cycle, physiological, morphological, and behavioural attributes in response to the influence of flow variability at evolutionary to local patch scales (Hynes 1970; Gray and Fisher 1981; Fisher *et al*. 1982; McAuliffe 1983; Minshall and Petersen 1985; Poff and Ward 1989; Lytle and Poff 2004).

Not surprisingly, all flow components and criteria identified as central elements of a river's flow regime (Section 1.4.2) have been identified as important aspects of disturbance, with debate as to which might be of primary importance, particularly recognising differences in response expected across various groups of organisms (Minshall 1988; Statzner *et al.* 1988). Furthermore, as Poff and Ward (1989) pointed out, it is extremely difficult to unravel the relative contributions of different hydrologic variables to the overall selective forces operating in rivers, as such contributions are temporally (and spatially) variable (see Section 4.1, for further discussion). Palmer *et al*. (1997) and Palmer and Poff (1997) emphasised the potential of measures of variance *per se* in explaining how changes in ecological pattern or process may be linked to flow variability. Palmer *et al*. (1997, p. 192) noted that "*variability* in flow over time or space has been shown to influence the distribution of stream biota even if flow never exceeds critical thresholds typical of floods". Until very recently, certainly, few studies had assessed the impact of flow regime on aquatic biota on the basis of multiple measures of flow simultaneously, or with due attention to aspects of flow variability (but see Section 4.1 and Chapter 8).

Resh *et al*. (1988) made one of the first concerted attempts to link flow disturbance and predictability, using a statistical approach (Figure 1.4), to show that hydrological events may be considered disturbances only if, for a specific time period, they are extreme relative to some expected longer-term average condition. They argued that, as shown for two hypothetical streams in Figure 1.4, temporal seasonal flow variability influences whether or not a high flow could be considered a disturbance within a river, with the same magnitude flow event plausibly representing a disturbance in one system but not in the other. Accordingly, flood events (a) and (c) (Figure 1.4) were within the normal seasonal variation (i.e. within arbitrary ± two standard deviations of flow predictability – for illustration purposes; see the valid critique by Poff 1992). In contrast, (b) and (d) were viewed as disturbances by Resh *et al*. (1988), as they fell outside the defined limits of predictability. Although of identical magnitude, discharge (c) therefore was not a disturbance while (d) represented an unpredictable high flow.

In situations therefore where flow events are highly predictable, such as a regularly timed spring flood in high-altitude snowmelt rivers, or fall well within the realm of natural flow variability, it has been concluded by some researchers that they cannot be considered disturbances (e.g. Wallace 1990). This notion is not

widely held nowadays and has been challenged by Poff (1992) and others (Section 1.4.3). It is generally accepted, nonetheless, that so-called 'unpredictable disturbances' are liable to exert a greater ecological impact than more predictable ones of similar magnitude (Resh *et al*. 1988; Poff 1992). For example, a high discharge occurring at an unusual time of the year (in evolutionary or historical terms) would be expected to exert a greater potential impact ecologically than the same flood occurring at the usual time (Poff 1992).

Hydrological statistics, such as those presented in Figure 1.4, have utility in characterizing the predictability of streamflow generally, facilitating among-river comparisons of hydrological regimes - an important part of ecohydrological research nowadays (and an integral aspect of this thesis; Chapter 4). Such statistics, as Poff (1992, p. 87) validly pointed out, however, are arbitrarily selected and "cannot necessarily be used to characterize the predictability of the *disturbance* specifically." Similarly, although formal measures of predictability (e.g. Colwell's indices; Chapter 4) can be used effectively to demonstrate differences in the temporal distribution of extreme flows across rivers that may constrain the biota in different ways, they do not automatically describe predictability of disturbance *per se*; the minimum or maximum monthly extremes from which such measures are derived are arbitrary, in that they do not necessarily represent actual hydrological disturbances (Poff 1992).

Poff (1992) rightly emphasised the need for non-arbitrary, objective criteria for disturbance in order to characterize the statistical predictability of a disturbance regime in a manner that satisfies accepted disturbance definitions. It is also essential that the scale of observation is specified, both for the characteristics of the physical disturbance and the ecological level(s) of response (see above). Then, once a particular "threshold disturbance flow" is established, the statistical properties of a disturbance regime can be determined from available hydrological data (Poff 1992, p. 88). For example, Poff (1992) proposed channel-wide (e.g. bankfull discharge, often correlated with sediment transport and active channel maintenance) and finer-grained, patch-specific (e.g. level of flow resulting in patch-specific disruption) approaches "to identify threshold flows that potentially constitute ecologically meaningful physical events."

Addressing flow disturbance from the above perspective ensures that specific flow events are linked explicitly to particular system characteristics, promoting ecologically relevant descriptions of disturbance regimes. It also facilitates spatial and temporal comparisons of ecological response to specific flow events within and across rivers. An attempt was made to adopt such an approach in this thesis, where simple bounds on natural long-term flow variability were established to assess whether or not a particular reduction in flow potentially constituted a disturbance to invertebrates (Chapter 4), disturbance was defined in terms of physically relevant flow-related events (Chapter 6), and ecologically meaningful responses sought (Chapters 7-8).

It was readily apparent from many of the studies reviewed for this thesis, that researchers have not found it easy to make distinct what constitutes an ecologically meaningful disturbance, outside the natural realm of

system variability, when dealing with flow. In the past, the importance of flow variability to riverine biota was emphasised (e.g. Hughes and James 1989; Poff and Ward 1989), but river ecologists made poor use of the potential information on flow disturbance held in historical flow records (Jowett and Duncan 1990; Hildrew and Giller 1994). The situation has changed over the past decade particularly, with a wide range of hydrological variables having been used to describe aspects of the disturbance regime of rivers, in terms of overall flow variability, as well as specific characteristics of floods and low flows (see below and Section 4.1, for further discussion). Much remains to be done, however, in linking flow regime dynamics to ecosystem response and the very large number of potential measures of flow disturbance makes the selection of ecologically significant indices extremely difficult (Olden and Poff 2003; Section 4.1).

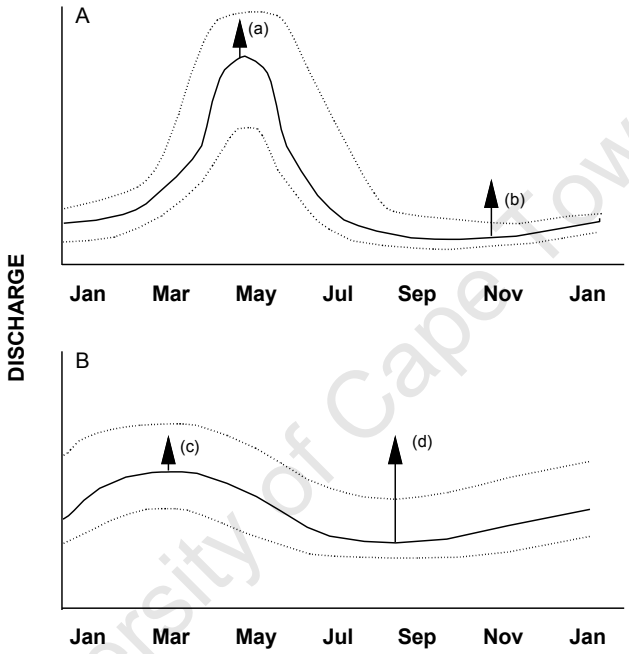


Figure 1.4 Discharge as an example of disturbance, for two hypothetical streams with different natural hydrological regimes: A - Rocky Mountains, western U.S.A.; B - Piedmont stream, southeastern U.S.A. (from Resh *et al.* 1988). Discharge is shown as a solid line, with an arbitrary ± 2 S.D. of predictability represented by dashed lines. Arrows (a)-(d) represent peak flow events.

Both high flows and low flows, particularly extremes such as prolonged low flows or zero-flow conditions that may result in drying or, at the other end of the spectrum, floods, exhibit high potential as disturbances and thereby play a central role in structuring stream communities (Ward 1982; Stanford and Ward 1983; Boulton and Suter 1986; Resh *et al.* 1988; Grimm and Fisher 1989; Frid and Townsend 1989; Reice *et al.* 1990; Hildrew and Giller 1994; Poff and Allan 1995; Poff *et al.* 1997). The coexistence of different riverine invertebrate species is dependent, in part, on the ecological differences among species in their responses to flow disturbances that operate within a generation time (Hildrew and Giller 1994). "In effect, disturbance is acting as a niche dimension for species, and they are ecologically separated along it, some species dominating undisturbed local patches, others persisting in disturbed patches nearby (Hildrew and Giller

1994, p. 48); an example of small-scale changes in the flow field potentially generating localised, underexploited patches in space or food was used.

General supporting evidence for flows as disturbance is documented in, among others (see also Section 1.3): Hynes (1970); Vannote *et al*. (1980); Stanford and Ward (1983); McAuliffe (1983); Ward and Stanford (1983b); Fisher (1983); Boulton and Suter (1986); Meffe and Minckley (1987); Minshall (1988); Resh *et al*. (1988); Power *et al.* (1988); Delucchi (1988); Jowett and Duncan (1990); Fisher and Grimm (1991); Quinn and Hickey 1994; Death and Winterbourn (1995); Poff and Allan (1995); Death (1996a, b); Bournard *et al.* (1996); Puckridge *et al.* (1998); and Bunn and Arthington (2002).

Poff and Ward (1989) speculated that with perennial systems, the flood regime probably is of primary importance in structuring communities in relation to the river habitat templet, coining the term 'flow template' (Section 1.4.5). Certainly, particular attention has been directed at studies of higher flows and specific flood events as disturbances for invertebrates, many by quantifying disturbance in a geomorphological context in terms of natural physical movement of the stream bed during flood events (e.g. Fisher *et al.* 1982; Fisher 1983; Resh *et al.* 1988; Minshall 1988; Townsend 1989; Scrimgeour and Winterbourn 1989; McElravy *et al.* 1989; Rader and Ward 1989; Lake *et al.* 1989; Doeg *et al*. 1989; Yount and Niemi 1990; Cobb *et al*. 1992; Palmer *et al*. 1992; Boulton and Lake 1992b; Death and Winterbourn 1994; Townsend *et al*. 1997a; Downes *et al*. 1998a; Lake 2000; Silver *et al*. 2004).

In contrast, the roles of droughts and other extreme low flows have been largely neglected (Resh *et al*. 1988; Fisher and Grimm 1991; Grimm 1994; Poff *et al*. 1997; Lake 2000; Humphries and Baldwin 2003; Section 7.1). Such events also are often assumed to represent a comparatively minimal disturbance to benthic invertebrates (e.g. Lancaster *et al*. 1990; Downes *et al*. 1998b). Milner (1994, p. 89) made the observation that "In contrast to floods, drying of stream channels normally occurs gradually and thus many species have evolved life history or behavioural adaptations for rapid recovery when flow returns." Townsend (1989) felt that low discharges generated small-scale disturbances which could be quickly compensated for through recovery mechanisms, while flood events could be considered large-scale disturbances to a river system. Townsend (1989, p. 44) also stated, however, that "Many questions remain to be answered about community dynamics in low discharge periods." Such uncertainty remains, despite increasing attention being paid to low-flow disturbance (Section 7.1).

1.4.5 The river habitat templet and flow

Habitat templet of a river

The long-term regime of natural environmental heterogeneity and disturbance in time and space (Section 1.4.3), constitutes a (river) habitat templet (or template; *sensu* Southwood 1977, cited in Poff and Ward 1989; Southwood 1988; Minshall 1988; Hildrew and Giller 1994). Differences in the selective forces acting on the habitat template and on ecological response to disturbance are understood to exist among rivers, as a

function of variations in features ranging from climate and biogeography to local habitat and community structure (e.g. Fisher 1983; Peckarsky 1983; Fisher and Grimm 1988; Poff and Ward 1990; Hawkins *et al*. 1993). The templet's axes of spatial and temporal heterogeneity influence the combination of genetic, life history, physiological, behavioural and other attributes that constrain local species persistence and community organization (Stanford and Ward 1983; Poff and Ward 1990; Scarsbrook and Townsend 1993; Townsend and Hildrew 1994; Poff and Allan 1995; Townsend *et al*. 1997a; Poff 1997). Species with traits conferring resistance or resilience (Section 1.4.3) are expected to increase in importance along the axis of increasing temporal variation (Minshall 1988; Townsend and Hildrew 1994; Townsend *et al*. 1997a). Increased spatial heterogeneity is thought to ameliorate or modify the impact of disturbances, not least through the provision of refugia (Section 1.4.3), so that species lacking in such resistance or resilience traits might still persist at least in moderately disturbed habitats.

The challenge of linking responses and biological traits of organisms with the heterogeneity, predictability and/or productivity of their habitats, to develop habitat templates for different ecological responses, has been taken up by various researchers from the 1980s onwards (Stanford and Ward 1983; Hildrew and Townsend 1987; Minshall 1988; Resh *et al*. 1988; Power *et al*. 1988; Poff and Ward 1990; Townsend and Hildrew 1994; Townsend *et al*. 1997b; Statzner *et al*. 1997; Dolédec *et al*. 1999). For example, Statzner *et al*. (1997), using world-wide data on the reproductive biology of 131 species of aquatic insects in relation to gradients of habitat heterogeneity, demonstrated that habitat acted as a template for life history traits of species, and for reproductive strategies in particular. While trends between the habitat template and species richness, for example, were demonstrated to conform to theory in this and other studies (e.g. Stanford and Ward 1983; Scarsbrook and Townsend 1993; Poff and Allan 1995; Townsend *et al*. 1997a), others, such as Resh *et al.*'s (1994) long-term study of species traits and habitats of the Rhône River failed to support anticipated theoretical predictions. Poff (1997) presented a framework (niche model) for understanding and predicting distributions and abundance of lotic communities that explicitly considers the functional relationships of species, based on species traits as predictors, with different nested habitat 'filters' from microhabitat to river basin; examples were presented for species traits presumed to reflect functional relationships with flow-related phenomena.

The theory on species life history traits in relation to the nature of the river habitat template, as well as studies of species response to flow disturbances (Section 1.4.4), have lent support to the notion that populations and assemblages within rivers exhibiting high levels of variability and spatiotemporal heterogeneity and low predictability, would be less susceptible to disturbance, relatively speaking, than those of more constant and/or contingent systems.

Flow - a determinant of the habitat templet

Flow regime variability over time, and the disturbance mediated through various flow events, are widely considered a primary determinant of the habitat templet (Minshall 1988; Poff and Ward 1989; Townsend and

Hildrew 1994; Richter *et al.* 1996, 1997a; Stanford *et al.* 1996; Puckridge *et al.* 1998; Bunn and Arthington 2002). Poff (1996, p. 72) observed that "hydrological *variation* has come to be viewed as an important element of the habitat template" and Poff *et al.* (1997, p. 772) went so far as to state that the habitat template "is dictated largely by flow regime". Bunn and Arthington (2002) drew on habitat template theory in examining the influence of a river's flow regime on physical habitat, the availability and suitability of which in turn influence biotic composition and diversity (Section 1.4.5). Further, they used it to examine how flow modification altered catchment- to patch-scale habitat, creating novel conditions to which native biota might be poorly adapted.

Minshall (1988, p. 278, Figure 4) adapted the habitat templet model for flow-related disturbance in streams, with the axes identified as change in flow (e.g. magnitude of change in discharge over a previous level) and flow predictability (the pattern, or lack thereof, of discharge variation over time). The templet axes were explored in relation to various species strategies for communities, and thus probabilities of biotic versus abiotic control with flow disturbance (Section 1.4.3). Poff and Ward (1990) developed a theoretical model of the ways in which environmental heterogeneity and disturbance provided a physical template for species persistence. Disturbances were treated as 'signal intensities' potentially beyond the species-specific, tolerance ranges of individuals, exerting increasing influences on species fitness and performance as their intensity and duration increased. The case was presented that natural variability in physical and chemical conditions and disturbances are distributed within statistically definable limits that can be expressed relative to the life cycle characteristics of the biota. The ability of species to persist would depend on them either possessing life history or behavioural characteristics enabling them to avoid harmful conditions, or on their degree of tolerance, over different life history stages, for the range of conditions present; tolerance levels might be reduced, due to protracted adverse conditions. Structural habitat complexity was recognised as potentially further increasing species' tolerance by providing refuges. Townsend *et al*. (1997b) found that species richness and traits representation across 35 insect taxa from 54 tributary sites on the Taieri River, New Zealand, conformed to original theoretical predictions (Townsend and Hildrew 1994), in an assessment of how well habitat templet theory addressed spatiotemporal heterogeneity driven by flow disturbance regime. A temporal axis of disturbance intensity/frequency (in terms of bed movement during high flow events) and a spatial axis that comprised a multivariate flow refugium index defined the habitat templet.

Certainly, acquaintance with the history of flow disturbance acting on the habitat template was acknowledged in this thesis as central to understanding invertebrate response to low flow dynamics (see Chapters 4-8).

1.4.6 Habitat patch dynamics – relationships with disturbance and flow

Patch dynamics is an appropriate unifying theory for rivers that borrows much from the principles of terrestrial landscape ecology (Hildrew and Giller 1994), where the spatial interrelationships of patches and the dynamics of the resultant broader landscape mosaic are examined in relation to the effects of natural or

anthropogenic disturbances (Sousa 1984; Pringle *et al*. 1988; Armitage *et al*. 1995; With *et al*. 1997). The theoretical basis of 'patch dynamics' (*sensu* Thompson 1978, cited in Pickett and White 1985) and 'hierarchical patch dynamics' (*sensu* Wu and Loucks 1995), as well as the various forms of and contributors to patchiness in rivers remain widely discussed (e.g. White and Pickett 1985; Pringle *et al*. 1988; Townsend 1989; Frid and Townsend 1989; Poff and Ward 1990; Kotliar and Wiens 1990; Hildrew and Giller 1994; Townsend and Hildrew 1994; Death and Winterbourn 1995). Downes (1990) provides a critique of patch dynamics models.

In contrast with terrestrial landscapes, there has been inadequate investigation by lotic ecologists of the dynamic nature of patch mosaics, and of the interactive processes that govern their form and function, as well as of disturbance-induced changes in stream patchiness (Pringle *et al*. 1988; Palmer *et al.* 2000; Lake 2000; Silver *et al*. 2004). The view that river habitats, as well as resources and biota, comprise patches in the landscape that are dynamic in space and time has, however, attained credibility over the past decades (Sousa 1984; Pickett and White 1985; Pringle *et al*. 1988; Barmuta 1989; Townsend 1989; Downes 1990; Levin 1992; Downes *et al*. 1993; Hildrew and Giller 1994; Wu and Loucks 1995; Lake 2000). Such patches can change in location, dimensions, boundary distinctness, as well as in time and in terms of the mechanisms responsible for in-patch and among-patch change, thereby constituting "parts of an ever-changing mosaic" (Lake 2000, p. 578). Pringle *et al*. (1988, p. 504) added that "Viewing streams as mosaics of patches provides a fresh perspective for lotic studies", allowing quantitative comparisons within and across rivers that yield information central to river management.

Definitions and a framework for patch dynamics

Wu and Loucks (1995) reviewed the varied definitions of a patch and patchiness, all of which are dependent on the system context and the explicit scale at which it is viewed (Downes 1990). Although current notions of patchiness remain vague (Cooper *et al.* 1997), in broad terms a patch refers to a spatial unit that differs from its surroundings in nature or appearance (Wiens 1976, cited in Wu and Loucks 1995; Pickett and White 1985; Kotliar and Wiens 1990). Pringle *et al*. (1988, p. 505) presented an operational definition of a patch as "a spatial unit that is determined by the organism(s) and problem(s) in question", recognising the significance of different spatial and temporal scales, and from coarse-to fine-grains.

Pringle *et al*. (1988), in providing a fundamental framework for applying patch dynamics to river research, emphasised the importance of: defining a patch unit appropriate for the scale of variation perceived or exploited by the organism (or process) under study, and the scale at which patch-to-patch variation was affected by the organism/process; examining key patch characteristics and process-orientated patch interactions within the broader context of the river landscape; and selecting sampling units, timeframes and approaches of appropriate scale. The need to select "biologically-meaningful patch sizes" for study (Downes 1990, p. 413) was also highlighted by Townsend (1989), Wiens (1989) and Palmer *et al.* (2000). In this

thesis, biotope patch characteristics were assessed in terms of their hydraulic (Chapter 6) and biotic relevance (Chapters 7 and 8).

Wu and Loucks (1995) built on Pringle *et al*.'s (1988) general conceptual framework, identifying five major elements of 'hierarchical' patch dynamics. Ecological systems were envisaged as nested, discontinuous hierarchies of patch mosaics (i.e. systems of patches that differ in size, shape and succession stage at particular scales), and with dynamics that are a composite of the dynamics and interactions of constituent patches on different scales. It was recognized that a range of processes could create, maintain, alter or demolish pattern, and that pattern could either constrain or facilitate ecological processes.

Patch characteristics and metrics

Numerous aspects of patch character, and hence metrics, have been identified as of potential importance in assessing the ecological effects of flow disturbance within the riverscape (Sousa 1984; White and Pickett 1985; Pringle *et al*. 1988; Hildrew and Giller 1994; Wu and Loucks 1995; With *et al*. 1997; Waddle 1998a; Palmer *et al*. 2000; Silver *et al*. 2004). These include: size; geometry; perimeter to area ratio; internal heterogeneity (structural complexity); content; number, diversity and size distribution; location, proximity to colonist sources, spatial arrangement and juxtaposition; time of creation; boundary characteristics, including total amount of patch edge (increases with patch area and is also affected by patch geometry); duration; mechanisms affecting patch formation; largest cluster size (and amount of edge around it); percolation frequency (ability of organisms to traverse the landscape); and correlation length (average distance between two sites belonging to the same cluster, and a measure of connectivity).

Patch connectivity

In addition to individual patches, the pattern of the entire mosaic of patches and the central issue of their connectivity (i.e. extent of habitat fragmentation; Taylor *et al*. 1993), has become a necessary area of study (Cooper *et al.* 1997; With *et al*. 1997; Palmer *et al.* 2000). Connectivity (in this study, of the reach biotope mosaic) refers to the functional interrelationships among habitat patches as a result of habitat being physically adjacent (i.e. spatial contagion) and/or because the movement responses (dispersal abilities) of organisms, with various habitat affinities and resource needs, effectively connect various patches (With *et al*. 1997). Palmer *et al.* (2000) recognised that inter-patch connectivity in streams may be provided through the water column, rather than through continuous bottom habitat.

With *et al*. (1997, p. 151) noted that "Heterogeneous landscapes provide a particular challenge for modelling population-level responses to habitat fragmentation, because individuals may be utilizing multiple habitats to varying degrees across the landscape." Moreover, it is complex to disentangle the effects of the relative amount of habitat available versus the spatial arrangement of that habitat in the landscape. Whether or not a landscape is connected is not only dependent on habitat abundance and spatial pattern, but also on how species are able to use and move through the patches that define it and on their habitat specificity (Taylor *et*

al. 1993; With and Crist 1995; With *et al*. 1997). As a result, different organisms have differing perceptions of the extent to which the biotope mosaic is fragmented. Habitat specialists with limited dispersal capabilities might possess far lower thresholds to habitat fragmentation than more vagile taxa or effective dispersers, which might be able to perceive and operate within the landscape as functionally connected across a greater range of fragmentation severity (With and Crist 1995; With *et al*. 1997). With and Crist (1995) showed by simulation modelling, that for habitat specialists with a minimal dispersal range, landscape connectivity was less important than the absolute abundance of habitat required. For habitat generalists, percolation across the landscape was a function of dispersal range and degree of habitat association.

Based on modelling comparisons of random habitat maps, in which the distribution of habitat is spatially independent, and fractal maps, in which habitat exhibits an intermediate level of spatial dependence (more akin to the real situation on a river bed), the spatial arrangement of habitat was found to be the most important factor structuring population distribution patterns (With *et al*. 1997). At fine scales, habitat abundance determined population dispersion in both models, but at coarser scales in fractal landscapes population distribution was primarily influenced by species' habitat affinities. The differential interaction of species with landscape structure (i.e. different residence probabilities in each habitat type) was found to be the primary determinant of distribution patterns, when the independent effects of habitat carrying capacity and habitat affinity on population distributions were assessed.

Patch dynamics, disturbance and the habitat templet - effects of patchiness on biota

Pickett and White (1985, p. 4) observed that patch dynamics theory is strongly interwoven with disturbance (Section 4.1.3) and habitat template theory (Section 1.4.5), such that "Most disturbances produce heterogeneous and patchy effects" the ecological consequences of which are dependent on various aspects of the biophysical pre-disturbance state of the system. The salient point, that "Hierarchical patch dynamics emphasizes, rather than avoids, the importance of disturbances, heterogeneity, and multiple spatiotemporal scales in managing or conserving ecological systems" (Wu and Loucks 1995, p. 460), has been recognised by others (e.g. Townsend 1989; Frid and Townsend 1989; Scarsbrook and Townsend 1993; Hildrew and Giller 1994; Matthaei and Townsend 2000).

Reice *et al*. (1990, p. 656) emphasised that "disturbance is the basis of stream patchiness", resulting in a mosaic of patches in different stages of succession, rather than the phased patch responses anticipated to occur in more homogeneous settings (Levin and Paine 1974, cited in Poff and Ward 1990). Pickett and White (1985) noted the possibility that local patches of different habitat character might respond differently to the same disturbance regime (examined in the present study through flow-related biotope dynamics; Chapter 6). Lake *et al.* (1989) highlighted the importance of differentiating between disturbed patches within a greater landscape of occupied or unoccupied habitat. Poff and Ward (1990) postulated that the temporal persistence of patches depended on disturbance frequency and on patch susceptibility to

disturbance. The discussion and theory of disturbance effects within and among patches continue to evolve (e.g. Collins and Glenn 1997; McCabe and Gotelli 2000).

Wiens (1989), With *et al*. (1997) and others have underscored the importance of adopting an organism-centred view of patch dynamics on the basis of criteria such as habitat affinity, response to habitat heterogeneity in terms of movement behaviour, habitat quality, and its ultimate consequences for fitness (as done in this thesis, by examining the biotope affinities of various taxa and their relationships with biotope dynamics; Chapters 7 and 8). Patchiness may affect invertebrates in ways that: strengthen or reduce resistance (Peterson and Stevenson 1992), altering the rate and pattern of post-disturbance recovery (Peterson and Stevenson 1992; Townsend *et al*. 1997b), with certain patches critical for the persistence of individuals including through the provision of refugia (Townsend and Hildrew 1994; Townsend *et al*. 1997a; Lancaster and Hildrew 1993a, b; Hildrew and Giller 1994; Palmer *et al.* 2000); confer community stability (Pringle *et al*. 1988) and maintain biotic diversity, with the juxtaposition of a high diversity of patches of differing resource character, complexity and boundary conditions (Naiman *et al.* 1988) at different stages of recovery from disturbance (Pickett and White 1985; Palmer *et al.* 2000); and alter the outcomes of abiotic and biotic interactions in rivers (McAuliffe 1983; Power *et al*. 1988; Townsend and Hildrew 1994). Poff and Ward (1990) observed that the close, intricate association of benthic macroinvertebrates with the substratum conferred particular ecological importance upon spatial heterogeneity at smaller patch scales (e.g. microhabitat), particularly in relation to their ability to respond to natural variability or disturbance events. Scarsbrook and Townsend (1993, p. 408) considered that "quantification of invertebrate patchiness before and after disturbance events coupled with physical measurements will provide valuable information on the links between invertebrate retention and patch characteristics" (Chapters 6 and 7).

Flow-related habitat patchiness

Hildrew and Giller (1994, p. 41) stated that "Undoubtably the major architects of physical patchiness in streams are the forces of flow" (Section 1.4.7). Flow extremes, as major disturbances, alter patches most dramatically, reconfiguring them and their linkages, thereby setting the stage for new pathways of patch development (Lake 2000). Although the effects of floods are fairly well studied in terms of patch dynamics, those of droughts (Lake 2000) and other low flow events have been largely neglected, this despite the fact that the latter events may also generate new spatiotemporal patterns of habitat patchiness, including through fragmentation. While major floods may disturb the entire river, flow increases and floods at smaller scales tend to disturb habitat patchily (Doeg *et al.* 1989; Lancaster and Hildrew 1993a; Death 1996b). A disturbance effect at low flows might similarly be expected to exert a patchy effect on habitat, and at similar patch scales. Davis and Barmuta (1989) and Lake (2000) recognised the dynamism of (micro)habitat patches even under such conditions of steady discharge where patch positions and boundaries may change, and where patch edges might be of particular importance in intercepting the flow.

Many interacting, flow related factors are known to generate the scale-dependent habitat patchiness in rivers to which invertebrates respond (Davis and Barmuta 1989; Davis and Growns 1991; Hildrew and Giller 1994; McAuliffe 1984), including substratum conditions and patterns of depth and velocity, and the resultant types of habitats/refugia of different hydraulic character (Newbury 1984; Lancaster and Hildrew 1993a, b; Clausen and Biggs 1997; Townsend *et al.* 1997b). Lotic ecologists have attempted to address the implications of such patchiness for invertebrate assemblages in part by delimiting relatively homogenous units for study, for example from riffles and pools, through to finer-scale patterns of habitat hydraulics (Pringle *et al*. 1988; Sections 1.4.6 and 1.4.7, see also Chapters 6-8). Lake (2000) postulated that at a regional scale, hydrology and geomorphology interact to generate a flow regime with a distinctive disturbance pattern that might influence species richness at this scale and generate pools of potential colonists for different habitat patch types. Hence, the fauna for each habitat type might be drawn selectively from a regional pool while, at the local scale of the patch type, interactions such as competition for resources might regulate local diversity.

1.4.7 A geomorphological context for flow-related physical habitat

It is well established that the interaction of fluvial geomorphology and flow regime controls river channel habitats, but in the past little attention has been directed at the appropriate spatial and temporal dimensions, and, even less so at the biological validation, of that interaction. In particular, greater effort is required to systematically integrate geomorphological and hydrological drivers into models for assessing river disturbance and its ecological consequences (Poff *et al*. 2006a, b). In this regard it is generally agreed that the physical habitat scale should be a focus of applied research for more effective river management (Harper and Everard 1998), enabling flow, geomorphic setting and hydraulic habitat characteristics to be related to biological diversity and processes, as well as to the biophysical consequences of flow disturbance (Section 1.4.5; Minshall 1988; Ward 1989; Kershner and Snider 1992; Hildrew and Giller 1994; Wood *et al*. 1999; Newson and Newson 2000; Parsons *et al*. 2004). As Whittington (2000, p. 16) observed "How habitat is influenced by alterations in flow is critical to understanding the biological outcomes of river management", a point challenging geomorphologists, ecologists and hydrologists to examine more interactively, and in greater detail, the nature of physical habitat (Newson and Newson 2000). Indeed, a hierarchical approach to categorize physical habitat is employed in many ecohydrological studies and environmental flow approaches currently in use (Kershner and Snider 1992; Section 1.5).

Frissell *et al.* (1986) defined perhaps the best known basis for habitat classification, a five-tiered model that linked the stream system (spatial scale of 10^3 m, temporal scale 10^6-10^5 years) to its habitat subsystems (viz. segment, reach, pool/riffle and microhabitat systems; spatial scales from 10^2 to 10^{-1} m, temporal scales from 10^4-10^{-1} y). Microhabitat subsystems were defined as "patches within pool/riffle systems that have relatively homogeneous substrate type, water depth, and velocity" (Frissell *et al.* 1986, p. 208; see below for further discussion of patch units). Spatial and temporal organization, and the processes controlling habitat, of any level of the system are constrained hierarchically by those of the level above and the manner in which habitat

change at higher levels exerts downward-cascading effects (see also Minshall 1988; Poff and Ward 1990; Kershner *et al*. 1992; Townsend *et al*. 1997a; Hildrew and Giller 1994; Parsons *et al*. 2004).

Wadeson and Rowntree (1994) and Rowntree and Wadeson (1997, 1998) expanded Frissell *et al.*'s (1986) model to produce a geomorphological framework well suited for ecohydrological applications, particularly environmental flow assessment (Section 1.5). It comprises six, spatially nested levels of functional organisation (viz. catchment, zone, stream segment, channel reach, morphological unit and hydraulic biotope). For this thesis, attention was focused on the smallest spatial-temporal scales nested within the stream reach and morphological unit (i.e. hydraulic biotope and microhabitat, < 1-10 m^2), and from a short-term geomorphic perspective. Newson and Newson (2000) proposed similar revisions to Frissel *et al*.'s (1986) hierarchy for habitat survey and modelling purposes. They used the term 'patch' to represent the microscale unit of channel habitat, defined by the biota in terms of substratum-flow interaction and sampled at the smallest hydraulic unit of a 'cell'. At the mesoscale (see below and Chapter 6), 'biotope' (defined by surface flow type or Froude number) was proposed, measured by transects or long-profile surveys. Hawkins *et al*. (1993) proposed a complementary hierarchical approach to facilitate greater understanding of habitat-biotic relationships, based on three increasingly fine scale descriptions of the morphological and hydraulic properties of channel geomorphic units (Section 6.1).

Parsons *et al*. (2004) discussed the importance of using both parallel hierarchy (i.e. a hierarchy of river system organization derived from fluvial geomorphology, as above) and self-emergence (i.e. no *a priori* imposition of scales of measurement, e.g. purely biological classification and ordination) approaches to detect meaningful hierarchical organization in multi-scale river ecological studies; such a combined approach was adopted in this thesis.

1.4.8 Stream hydraulic theory and ecohydraulics

At the scale of the reach "the influence of flow on the distribution of biota is often affected by changing hydraulic conditions rather than by any hydrological parameter *per se*" (Petts *et al.* 1995, p. 4). Interest in this scale of influence of flow in river ecology was renewed in the 1980s (Hildrew and Giller 1994) with the advent of "hydraulic stream ecology", a term coined by Statzner *et al.* (1988, p. 307) to reflect the empirical description of hydraulic habitat conditions experienced by instream biota. The theory evolved on the back of early efforts by Ambühl (1959, cited in Hildrew and Giller 1994), Edington (1965, 1968), Hynes (1970), and others to understand the mechanics of flow at local habitat scales in terms of its influence on invertebrate distributions and behaviour. It was increasingly influenced by the outcomes of studies that compelled lotic ecologists to revise earlier thinking on the nature and influence of the flow microenvironment (e.g. Davis and Barmuta 1989; Carling 1992).

Statzner (1981a), Statzner and Higler (1986), and Statzner *et al*. (1988) demonstrated the importance of hydrodynamics and stream hydraulics as key determinants of the distribution and abundance of benthic

macroinvertebrates across a wide range of spatial and temporal scales; it was also reflected that lotic organisms themselves may mediate changes in streamflow. Statzner *et al.* (1988) observed that hydraulics may be ordered in a nested hierarchy in much the same way as other river processes, for instance, with trends in hydraulic characteristics reflecting factors such as reach location and stream size (Section 1.4.7). Statzner and Higler (1986) proposed that wide ranging longitudinal variations in benthic invertebrate communities along rivers coincided with discontinuities in complex hydraulic variables. The spatiotemporal variability of hydraulic habitat and its various relationships with instream biota connect this area of study strongly with disturbance, patch dynamics and habitat template theory (Davis and Barmuta 1989; Poff and Ward 1990; Hildrew and Giller 1994).

Discussions of hydraulic stream ecology, near-bed hydraulics and the vast diversity of hydraulic variables considered in defining the microhabitat distributions and abundances of benthic macroinvertebrates, most commonly water depth, current velocity and substratum character, are provided in Statzner (1981a), Newbury (1984), Nowell and Jumars (1984), Minshall (1984), Davis (1986), Chance and Craig (1986), Statzner and Higler (1986), Statzner *et al*. (1988), Davis and Barmuta (1989), Statzner and Müller (1989), Davis and Growns (1991); Carling (1992), Campbell (1991, 1992); Young (1992); Gordon *et al*. (1992); Wadeson (1996) and Jowett (2003). A significant body of research has accumulated showing that both standard and more complex, integrated hydraulic indices (e.g. benthic shear stress) correlate well with the patchiness of distributions and abundances of a wide range of invertebrate taxa (see Section 8.1). As Carling (1992, p. 281) commented, "Given a multiplicity of hydrodynamic parameters, the question is which characterize the benthic ecological environment". Davis (1986), Davis and Barmuta (1989) and others have tried to address this question by classifying the near-bed flow regime in ecologically meaningful ways. For example, Davis and Barmuta (1989) provided an ecologically relevant classification of mean and near-bed flows in rivers based on a combination of descriptors of velocity, depth and substratum roughness that characterized five different flow microenvironments for the benthos.

The field of study has expanded over the past decade to allow for greater description and modelling of complex flow-hydraulic habitat dynamics and attempts at predicting implications for biota (Hildrew and Giller 1994; Poff and Allan 1995; Harper and Everard 1998; Newson *et al*. 1998; Hardy 1998; Jowett 2003). It is more commonly known nowadays as 'habitat hydraulics' (Norwegian Institute of Technology 1994) or 'ecohydraulics' (e.g. Leclerc *et al*. 1996). Debate still remains vigorous among proponents of ecohydraulics, however, as to the most valid scales and most appropriate variables for describing hydraulic habitat. Newson and Newson (2000, p. 198) noted that ecohydraulics remains "essentially a 'bottom up' field that assumes a knowledge of the habitat needs of all relevant communities of organisms, a knowledge which microscale studies are slow to provide" (see below). Pragmatically, therefore, a mesoscale approach (see below) appears most favoured (Armitage and Pardo 1995; Newson and Newson 2000, p. 200) "varying across the active channel width and at channel length intervals which are small multiples of channel width".

Ecologically relevant habitat units for benthic macroinvertebrates

Various researchers have constructed the above habitat hierarchy upwards from mesohabitat, to morphological unit, reach and higher scales, or downwards to microhabitat, to address in a standardised fashion the links among flow, habitat and biota (Harper *et al.* 1992; Harper and Everard 1998; Rowntree and Wadeson 1998; Kemp *et al.* 2000). Although agreement is still needed on hierarchical principles, terminology, and the geomorphological classification system within which an ecologically meaningful habitat typology could fit, a number of researchers have made important inroads, among them, Kershner and Snider (1992), Wadeson (1994, 1996), Rowntree (1996), Pardo and Armitage (1997), Newson *et al.* (1998), Padmore (1997), Cohen *et al*. (1998), Kemp *et al*. (2000), and King and Schael (2001). Typically, emphasis has been placed either on ecological (top-down) or geomorphological (bottom-up) fine-scale approaches, as compared in Newson and Newson (2000). Few studies have melded the two approaches, as done in this thesis (Chapters 6-8). Newson and Newson (2000, p. 213) observed that "The fusion of ecological and geomorphological expertise has obvious potential benefits for the urgently needed management tasks of setting ecological acceptable flows but will equally inform theoretical developments, such as the field of patch dynamics."

Geomorphological studies in several countries have demonstrated that patterns in ecohydraulics, at reach to patch scales, are controlled spatially by channel morphology and substratum composition (and by higher-level filters), as well as varying temporally with flow (Singh and Broeren 1989; Wadeson 1994, 1996; Heritage *et al*. 1996; Padmore 1997, 1998; Tharme and King 1998; Jewitt *et al*. 2001; Jowett 1998; Gippel and Stewardson 1998; Newson and Newson 2000; King and Schael 2001). Both empirical hydraulic geometry (i.e. reach and channel-width relationships with discharge) and within-reach mesoscale surveys are necessary to fully assess the spatiotemporal diversity of channel physical habitat and its gross scale features (Newson and Newson 2000; Section 6.1). Channel spatial units (patches – Section 1.4.6) typically have been defined *a priori*, both vertically and laterally, and then validated using various combinations of descriptors of hydraulic habitat. Increasingly, the extent to which they change in character and diversity across different flows (Chapter 6) and their biological relevance (Chapters 7 and 8) are also being assessed.

From a geomorphological standpoint, descriptions of habitat patches in relation to flow change have tended to be more focused on hydraulic characterization (see Chapter 6), typically, but not always, without biological validation. A physical or hydraulic biotope approach has particularly gained acceptance as a way forward (Newson *et al.* 1998). Broadly speaking, a 'biotope' represents a homogeneous environment that satisfies the habitat requirements of a biotic assemblage or community, recognizing the integration of those abiotic features that define the habitats of the individual species within it (Jowett 1993; King and Tharme 1994; Wadeson 1994, 1996; Padmore 1997; King and Schael 2001). This basic distinction has been recognised previously by numerous authors (see Wadeson 1994, for a full discussion). To differentiate between a biotope *sensu lato* and a patch of similar scale, but where the focus is entirely on flow-related abiotic features, Wadeson (1996, p. 9) coined the term 'hydraulic biotope' to represent a "spatially distinct

in-stream flow environment characterised by specific hydraulic attributes". Padmore (1997, 1998) used 'physical biotope' to reflect the same emphasis. Biotopes essentially occur as a series of spatially and temporally varying patches, the boundaries of which are delimited by hydraulic change brought about by the interaction between local reach morphology and flow.

In South Africa, research has focused on the flow-related dynamics of hydraulic biotopes (e.g. Wadeson 1996; Rowntree 1996; Wadeson and Rowntree 1998). Padmore (1997, 1998), Padmore *et al.* (1998) and Newson *et al.* (1998) similarly explored the utility of physical biotopes as a fundamental component of instream habitat for determining the conservation status and flow requirements of rivers in the U.K. Several researchers even found support for the generalised extension of hydraulic habitat or mesohabitat (see below) concepts to river segment and basin scales (e.g. Statzner and Borchardt 1994; Cohen *et al.* 1998; but cf. Newson and Newson 2000).

The hydraulic/physical biotope approach represents an important scalar link between the detail of microhabitat hydraulics and network-scale assessments of flow-habitat related river management, though one that needs to be far better informed through the inclusion of biologically validated biotopes or ecologically based mesohabitat approaches that evolved in parallel (King and Tharme 1994; Newson and Newson 2000; King and Schael 2001). Associations among biotope types and invertebrate assemblages have been explored in Palmer *et al.* (1991), King and Tharme (1994), Grundy (1996, cited in Newson and Newson 2000), Tharme and King (1998) and King and Schael (2001). In Chapters 6-8, the extent to which biotopes represented an appropriate patch unit for studying spatiotemporal change in physical habitat for invertebrates at low flows was a primary research focus.

Parallel ecological studies to those on biotopes led to the delimitation of anthropocentrically or management defined (Armitage *et al*. 1995) medium-scale habitat units, comparable in scale to (though perhaps somewhat larger in area than) their geomorphologically defined counterparts. These latter units, termed 'mesohabitats' or 'functional habitats' (e.g. Kemp *et al.* 1999, 2000; Harper *et al*. 1992; Pardo and Armitage 1997; Harper and Everard 1998; Vadas and Orth 1998) appear essentially synonymous, having developed in parallel research initiatives (Kershner and Snider 1992; Kershner *et al.* 1992; Kemp *et al*. 2000; Tickner *et al.* 2000). Harper and Everard (1998, p. 402, Figure 1) highlighted the importance of functional habitats in river habitat survey and management, as the interface between physical processes and instream biodiversity.

A mesohabitat has been defined as "a discrete unit of habitat at the pool/riffle scale that has distinct hydrologic and biological characteristics" (Kershner *et al.* 1992, p. 180). Pardo and Armitage (1997, p. 111) simply defined mesohabitats subjectively as "visually distinct units of habitat within the stream, recognizable from the bank and with an apparent physical uniformity" (see also Armitage and Pardo 1995; Armitage *et al*. 1995). Wood *et al*. (1999, p. 266) defined mesohabitats as "medium-scale habitats that arise through the interactions of hydrological and geomorphological forces (which may include instream macrophyte

growth)", and recognised their position in stream classification between microhabitats (e.g. a stone surface) and macrohabitats (which might include an entire reach). Vadas and Orth (1998, p. 143) defined mesohabitat types more specifically, as "moderately large habitat units that usually only occur once per meander (riffle-pool) sequence and are relatively homogeneous in hydraulic characteristics (e.g., fast riffle and shallow pool)", often delineated by sharp changes in surface turbulence and/or water depth. Harper *et al*. (1992) advocated the development of a building block approach to biological habitats, objectively differentiating functional habitats, from the mosaic of visually identifiable mesohabitats encompassing the entire wetted channel, as those inhabited by distinct invertebrate assemblages. Although Pardo and Armitage (1997) and Wood *et al*. (1999) stated that the term 'mesohabitat' introduces a scalar dimension which 'biotope' does not have, biotope studies do not support this view (e.g. Wadeson 1994; Padmore 1998; this thesis).

Newson and Newson (2000) observed that unlike biotope studies, mesohabitat/functional habitat research tended to be executed empirically, with limited reference to geomorphological principles or stream hydraulic theory. Certainly, in the past, ecologists intuitively related the distribution and composition of benthic invertebrate assemblages to different hydraulic habitat units or habitat types, such as pools and riffles, frequently differentiated on the basis of subjective criteria. Wadeson (1994, 1996) and Padmore (1997) comprehensively reviewed the surfeit of terms used to describe such instream flow environments of significance to the biota, as well as the diverse criteria on which they were based.

A hierarchical habitat approach with stratification on the basis of biotopes or mesohabitat/functional habitats has been identified as an alternative standard to habitat simulation procedures for environmental flow assessment (Kershner and Snider 1992; Tharme 1996, 2003; Tharme and King 1998; Wadeson and Rowntree 1998; Newson *et al.* 1998; Acreman and Dunbar 2004; Section 1.5). Newson *et al.* (1998, p. 444) proposed the following steps: problem scoping, with identification of key biota and probable critical habitats/biotopes; biotope mapping at a range of discharges; functional habitat mapping in major seasons; translation through habitat preference curves and hydraulic geometry studies to select appropriate areas and hydraulic conditions; and an outline of alternatives for flow (and/or channel) management to protect habitat. It is noteworthy that such a process has essentially evolved over time as one element of the backbone of the BBM and similar holistic methodologies. It also reflects significant aspects of the sequence of ideas in this thesis.

Although a fair amount of energy has been invested in categorizing physical habitat, especially from a geomorphological viewpoint, far less effort has been expended thus far on ascertaining the ecological meaning of such habitat characterization (Chapter 6). The latter topic is at the crux of this thesis, where an attempt is made to elucidate the ecological relevance of the dynamics of low flow habitat. Moreover, it is important in ecohydrological work, including environmental flow assessment (below), where there has been a marked shift from the use of simple hydrological indices or habitat-discharge relationships, as surrogates

for the requirements of the biota or ecosystem, to the identification of combinations of flow and habitat parameters of direct ecological significance.

1.5 INTERNATIONAL TRENDS IN ENVIRONMENTAL FLOW ASSESSMENT FOR RIVERS

Ongoing deterioration of the condition of riverine ecosystems stemming from flow alteration (Section 1.3) has provided the impetus globally (and in South Africa – Section 1.1) for an expanding field of applied research aimed at addressing the environmental flow requirements of rivers (EFRs), the science of environmental flow assessment (EFA) (Petts *et al.* 1995; Tharme 1996, 2003; Postel and Richter 2003; Dyson *et al.* 2003). Such research has evolved alongside, and with increasing exchange with, the contemporary river ecosystem theory on which it is founded (Section 1.4) - particularly the natural flow paradigm (Section 1.4.2), now widely acknowledged as an appropriate framework underpinning environmental flow assessment and river management (Richter *et al*. 1997a, 2003; Thoms and Parsons 2003; Poff *et al*. 2003).

This section outlines current international trends in the development and application of environmental flow methodologies for rivers, based on a full review conducted for the purpose of this thesis (see Tharme 2003). Further examination of approaches used specifically to assess and/or characterize ecologically relevant (low) flows for benthic macroinvertebrates is provided in Chapter 8.

1.5.1 Environmental flow assessment: concepts and origins

Environmental flow concepts

In the past, river ecosystem health and protection were predominantly a water quality issue (O'Keeffe 1995; Poff *et al*. 1997; King *et al.* 1999; Arthington and Pusey 2003) with a quantified allocation of water for the environment tending to be relegated to that water remaining after the requirements of all other users were met (i.e. 'surplus' or 'residual water'; Moore 2004). Nowadays, there is increasing acceptance worldwide that rivers have a right to freshwater (in both quantity and quality), alongside other uses of the resource that support social and economic welfare (Dunbar and Acreman 2001; Naiman *et al*. 2002; Arthington and Pusey 2003). Furthermore, environmental flow assessment is considered a fundamental element of an ecosystem approach to IWRM (Agarwal *et al.* 2000), intended to sustain river integrity and biodiversity while explicitly managing tradeoffs with other resource users (Dudgeon *et al*. 2006; Naiman *et al*. 2006). An international survey by Moore (2004) showed that close on 99% of respondents, from a wide range of water technical backgrounds, considered environmental flows a relevant concept for water resource management.

Although terminology is inconsistent, continuing to evolve with greater uptake of the practice, the term 'environmental flow' has been most commonly adopted to date (Tharme 2003; Moore 2004). An environmental flow assessment for a river may be thought of simply as an assessment of how much of the

original water regime should be provided to maintain or improve (through flow-related restoration) the condition of the river ecosystem (and any associated systems) and its benefits, typically where there are variously competing water uses and where flows are regulated (Tharme and King 1998; Tharme 2003; Dyson *et al.* 2003; Arthington and Pusey 2003; Postel and Richter 2003). Assessments may also be made for rivers or reaches with as yet unaltered flow regimes, but which are intended for future water resource developments, most commonly within regional, national or basin-wide audits for strategic planning (King *et al.* 1999; Tharme 2003).

Typically, a hierarchical approach to environmental flows has been adopted, at multiple levels of spatial scale and resolution, with different methodologies appropriate over such a broad scale range, as well as in accordance with time, data and other resource constraints (Tharme 1996, 2003; Arthington *et al.* 1998a; Acreman and Dunbar 2004; see Sections 1.5.3-1.5.6). The South African four-tier approach for ecological Reserve determination is one example, extending from rapid Desktop Estimate for the National Water Balance Model, at quaternary catchment scale, to a Comprehensive Determination (8-12 months), with extensive multidisciplinary field data collection, used for compulsory water licensing (DWAF 1999a, b). Hydrology-based methodologies tend to be applied for broad-scale basin planning purposes (Section 1.5.3), while either habitat simulation (Section 1.5.5) or holistic methodologies (Section 1.5.6) have been commonly used for more intensive environmental flow studies, for particular river systems or high priority reaches (Tharme 2003).

Historically, it was recognised that some amount of water needed to be left in rivers to provide habitat for the protection of economically important or endangered target species or to maintain water quality, particularly linked to limiting water abstraction during low flow periods (Tharme 1996; Petts 1996; Poff *et al.* 1997). It was commonplace, therefore, to recommend a single minimum discharge or volume, or a set of minima at seasonal or monthly time step, to achieve a singular environmental flow objective. The concept of a 'minimum flow', which provides limited scope for ecosystem protection, became entrenched as a result (Tharme 1996, 2003; Moore 2004). Since the late 1980s, in many parts of the world, it has been replaced by a more widely accepted vision of the provision of a recommended modified flow regime that mimics the natural flow pattern and timing as far as feasible (Section 1.2.1), linked to ecosystem management objectives or future development scenario(s) (Bunn and Arthington 2002; Tharme 2003). This new view has perpetuated a rather unrealistic expectation by some water experts that specific environmental flow prescriptions for rivers can be made rapidly and easily, but as Poff *et al*. (2003) and Arthington *et al*. (2006, p. 1312) rightly emphasised, "translating general hydrological-ecological principles and knowledge into specific management rules for particular river basins and reaches remains a daunting challenge".

Evolution of methodologies

Concerted development of methodologies for prescribing environmental flows for rivers began as early as the end of the 1940s, in the western U.S.A. Dramatic progress was achieved during the 1970s, primarily as a

result of new environmental and freshwater legislation, and demands from the water planning community for quantitative documentation of environmental flows (Stalnaker and Arnette 1976; Stalnaker 1982; Trihey and Stalnaker 1985), in concert with the peak of the dam-building era (WCD 2000; Rosenberg *et al*. 2000). Outside North America, the route by which methodologies became established for use is less well chronicled (Tharme 1996, 2003). In many countries, a structured environmental flow process only gained significant ground in the 1980s (e.g. England, Australia, South Africa) or later (e.g. Tanzania, Brazil, Czech Republic), while in several parts of the world, including eastern Europe and areas of Latin America, Africa and Asia-Pacific, the science remains poorly advanced (Tharme 2003).

1.5.2 Status of environmental flow practice and overview of methodology types

Current status of environmental flow practice

A recent global review of the status of environmental flow methodologies revealed the existence of some 207 individual methodologies of a number of various types, recorded for at least 44 countries within all six major world regions (Tharme 2003; Figure 1.5). Trends in methodology type by world region, as well as a synopsis of the methodologies adopted in individual countries, are provided in Tharme (2003). Although historically, the United States has been at the forefront of the development and application of methodologies for prescribing environmental flows, using 37% of the global pool of techniques, parallel initiatives in other parts of the world have provided the impetus for several novel advances in the science (Arthington 1998a; Tharme 2003; Sections 1.1 and 1.5.6). Just over half (52%) of the countries representing the developed world were shown to be routinely involved in environmental flow initiatives, while in developing countries the field of environmental flow research was nascent or only locally active, with only 11% of such countries recorded as applying methodologies by 2002 (Tharme 2003*)*. South Africa was found to be within the top ten most active countries in environmental flow research worldwide. Although the numbers of entirely new methodologies has levelled off (pers. obs.), the numbers of countries adopting environmental flow concepts and practice, as well as of case study applications, has continued to rise (10th International River Symposium and 2nd Environmental Flows Conference, Brisbane, Australia 2007; pers. obs.). Worldwide to date, however, environmental flow methodologies remain disproportionately focused on rivers and flow quantity, with the integral importance of flow quality often disregarded. Unfortunately also, the implementation of flows recommended for ecological purposes remains extremely weak (Tharme 2003; Poff *et al.* 2003; Arthington *et al*. 2006).

Overview of methodology types

The extensive body of methodologies that now exists for addressing environmental flows has been reviewed over time by numerous authors. Select recent critiques include those of: Karim *et al.* (1995); Tharme (1996, 2003); Jowett (1997); Stewardson and Gippel (1997); Arthington (1998a); Arthington and Zalucki (1998a, b); Arthington *et al.* (1998a, b); Dunbar *et al.* (1998); King *et al.* (1999); Dyson *et al*. (2003); Schofield *et al.* (2003); Acreman and Dunbar (2004); and Annear *et al.* (2004).

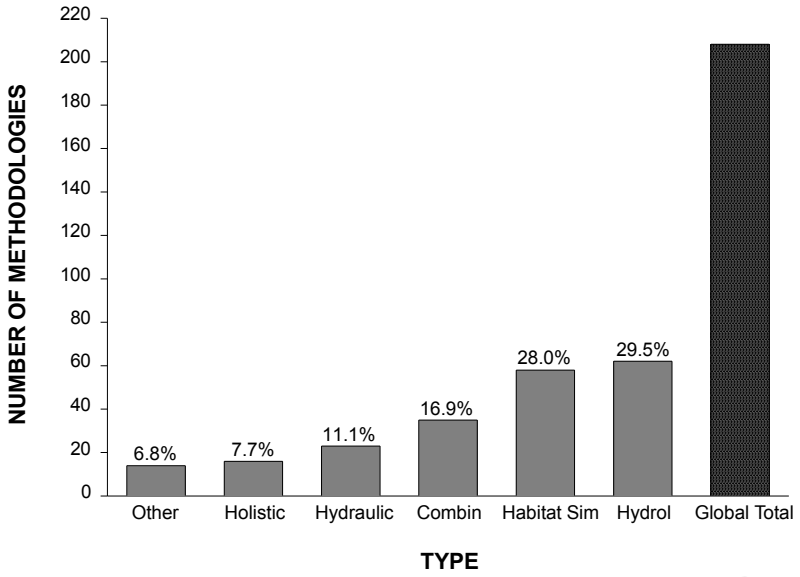


Figure 1.5 Number of environmental flow methodologies of each type in use worldwide and their relative proportions, compared with the global total (from Tharme 2003). Hydraulic - Hydraulic Rating; Combin - Combination; Habitat Sim - Habitat Simulation; Hydrol - Hydrological. Methodology types as discussed in the text.

The majority of EFMs described can be grouped into four (of six) reasonably distinct categories, namely hydrological, hydraulic rating, habitat simulation and holistic (or functional analysis) methodologies (Figure 1.5), although differences in classification exist (e.g. Loar *et al.* 1986; Gordon *et al.* 1992; Swales and Harris 1995; Tharme 1996; Jowett 1997; Dunbar *et al.* 1998; Dyson *et al*. 2003). Several other 'combination' or 'other' approaches that bear characteristics of more than one of the four basic types or represent alternative methods not developed specifically for EFAs, respectively, are reported from the literature (Figure 1.5; see Tharme (2003) for details). Examples include: managed flood releases (Acreman *et al*. 2000); multiple regression-based approaches (e.g. using the River Invertebrate Prediction and Classification System, RIVPACS; Wright *et al*. 1996); and the Basque Method, a biotic-hydraulic approach to environmental flows based on maintaining invertebrate and fish species diversity (Docampo and De Bikuña 1993). The use of physical biotopes or functional habitats, an approach of direct relevance to this thesis (Section 1.4; Chapter 6), has also been considered by several ecologists as an alternative environmental flow method (Section 1.4.8).

Although neglected in the past, because it was either incorrectly assumed that riverine invertebrates would respond to flow changes in precisely the same way as fish or that the food that they represent was not limiting for fish production (Orth 1987), methodologies from across all main types (Section 1.5.2) have been increasingly applied to determine flows for invertebrates, both as indicators of whole-ecosystem health or productivity and as a component of biodiversity (Campbell 1991, 1992; Tharme 1996; Choy 1998). Significantly, each approach has differed in the extent to which knowledge of the interrelationships among

flow, habitat and biotic response was central to the recommendations made, and in its scope for specifically addressing invertebrate low flow needs (Section 8.1 provides further discussion).

1.5.3 Hydrological methodologies

Basis and extent of application

Hydrology-based methodologies comprise look-up tables or other desktop approaches that rely primarily on hydrological data, in the form of naturalised, historical monthly or more commonly nowadays, daily flow records, for making environmental flow recommendations (Prewitt and Carlson 1980; Tharme 1996, 2003). Most commonly, a set proportion of flow, often applied only as a minimum flow (e.g. Cavendish and Duncan 1986; Milhous *et al.* 1989; Orth and Leonard 1990; Petts 1996) is derived from simple flow indices. Such indices include percentages of mean or average annual flow (MAF/AAF), or various exceedence percentiles calculated from flow duration curve (FDCs), which display the relationship between discharge and the percentage of time that it is equalled or exceeded (Gordon *et al.* 1992). The recommended flow is intended to maintain general river health, a freshwater fishery, or other highlighted ecological feature(s) at an acceptable level, on an annual, seasonal, or sometimes, monthly basis (Tharme 1996). Gordon *et al*. (1992), Stewardson and Gippel (1997) and Smakhtin (2001) reviewed many of the well established hydrological and regionalisation techniques used for gauged or ungauged catchments to derive the low flow indices typically used (e.g. Q_{95}, 7Q10, MAM(7); see Section 4.1). A few hydrological approaches have incorporated generalized hydroecological relationships for a catchment or catchment group (e.g. O'Shea 1995), and/or simple hydraulic, biological, or geomorphological criteria (e.g. Estes 1996; Ubertini *et al*. 1996).

Despite their obvious limitations (see below), hydrological approaches comprise the highest proportion of methodologies recorded globally at 30% (Tharme 2003; Figure 1.5). The majority of the 61 different hydrological indices or methods reported in the literature are still in use, though increasingly with various modifications to improve their ecological meaning and degree of transferability among different hydrological regions or river ecotypes.

The Tennant (Montana) Method, highlighted by Reiser *et al*. (1989b) as the second most widely used EFM in North America (at that stage used routinely in 16 states or provinces) has since become the most commonly applied hydrological methodology worldwide (Tharme 2003). Although superficially a standard-setting approach, the method, developed in the United States by Tennant (1976) and the U.S. Fish and Wildlife Service, differs from many other hydrological methodologies in that considerable field habitat, hydraulic and biological data were involved in its development. It comprises a table linking different seasonal AAF percentages to categories of flow-related river condition, as recommended environmental flows (Tennant 1976); the categories of condition range from "poor or minimum" (10% AAF) to "optimum range" (60-100% AAF). At least 25 countries have either applied the original method or a version modified on the basis of hydrological, geomorphological or ecological criteria (Dunbar *et al*. 1998; Annear *et al.* 2004), or have simply utilised various (often arbitrarily designated) AAF percentages (Tharme 2003). Estes

(1996) provided an example of a modification of the Tennant Method for Alaska, where fish ecology data, flow duration estimates and a mean monthly flow index were incorporated. Examples of the use of specific percentages of MAF to set environmental flows include 10% MAF in Spain (Docampo and De Bikuña 1993) and 2.5-5% MAF in Portugal (Alves and Henriques 1994).

Various flow percentiles and other single flow indices comprise the second largest subgroup of hydrological methods, applied in some 18 countries (Tharme 2003; see also Section 4.1). Probably the most commonly applied flow percentile, often at a seasonal level, is Q_{95}, applied for instance in Bulgaria, Taiwan and Australia (Tharme 2003). In the U.K., the Catchment Abstraction Management Strategies (CAMS) process, established to provide interim environmental flow estimates for water permitting, uses set percentages of the natural Q_{95} as an ecological river flow objective within a Resources Assessment and Management framework (Dunbar *et al.* 2004). The environmental sensitivity of the river system to flow change and hence, percentage of Q_{95} recommended, is based on a combined scoring system for four different ecosystem elements (viz. physical habitat, macroinvertebrates, fisheries, macrophytes). Other frequently applied, low flow indices include: Q_{90}, used in Brazil, Canada, and the U.K.; an index reflecting the consecutive 7-day low flow event of 1:10 year return period (7Q10; Pyrce 2004), direct percentages of which are applied across Brazil state-wide (Benetti *et al.* 2002), as well as in North America and Italy; and Q_{364} and similar indices, which have been used throughout Europe (Tharme 2003; Section 4.1).

More recent methodologies that more comprehensively characterize flow variability, and in a potentially more ecologically relevant way, include the Texas Method (Matthews and Bao 1991), Basic Flow Method (Palau and Alcazar 1996), and Australian Flow Translucency Approach (Gippel 2001). In the last approach, the natural flow regime is scaled down in magnitude, using various functions, whilst maintaining similar levels of flow variability, to produce a recommended regulated flow regime. For strategic water resources planning, as well as screening license applications for water abstraction, the South African Desktop Reserve model uses generic curves derived from the relationship between a composite index of flow variability (see Section 4.5), and high and low flow estimates from past BBM applications (Section 1.5.6), to determine the ecological Reserve (the EFR) (Hughes 2001; Hughes and Münster 2000; Hughes and Hannart 2003). The EFR can be calculated for different categories of future river condition (representing different degrees of departure from naturalness) and with different supply assurances. For example, drought requirements do not vary across categories of different river ecological condition, but are adjusted to be no greater than the natural minimum monthly flows. The model is also increasingly used as a tool during comprehensive BBM determinations, as well as in the context of limited ecological data for rivers in others parts of southern Africa.

Of the more recent hydrology-based approaches that have explicitly adopted ecohydrology principles (Sections 1.4.1 and 1.4.2), the Range of Variability Approach (RVA), primarily its component Indicators of Hydrologic Alteration (IHA) software (Richter *et al.* 1996, 1997a; The Nature Conservancy 2005), has been

applied most intensively since its inception, in numerous environmental flow-related studies in North America (Mathews and Richter 2007). It has also attracted interest in South Africa (e.g. Jewitt *et al.* 1999), England (Acreman and Dunbar 2004), and Australia (Arthington 1998a). In response to Bragg *et al.*'s (1999) conclusion that IHA/RVA was the most suitable environmental flow method for Scottish systems, Black *et al.* (2002) integrated a subset of IHA variables into a new Scottish method, the Dundee Hydrological Regime Assessment Method to assess the risk of impacts on riverine biota from flow regime alteration.

A sophisticated hydrology-based platform to address flow regime variability, RVA uses 67 different flow statistics commonly assessed in river studies due to their ecological significance and ability to reflect a wide range of types of flow alteration (Mathews and Richter 2007). It earned recognition as an holistic approach through ongoing efforts to correlate degrees of flow alteration with various ecological indicators (e.g. fish populations, riparian vegetation, species habitat) (Arthington 1998a; Puckridge *et al.* 1998; Bragg *et al.* 2005). The 33 core IHA statistics, as well as 34 others that reflect the main environmental flow components of holistic approaches (viz. extreme low flows, low flows, high flow pulses, small and large floods), are used interactively to explore flow-ecology relationships within numerous environmental flow assessments conducted in the U.S.A. using the Savannah or Ecologically Sustainable Water Management (ESWM) processes (Richter *et al.* 2003, 2006; Mathews and Richter 2007; Section 1.5.6). Targets for flow management are set as ranges of variation in each index or a subset of most ecologically meaningful indices, and can be monitored and refined over time to achieve the desired flow conditions, as well improve understanding of the dependencies of the ecosystem and its biota on flow variation. Puckridge *et al.* (1998) suggested that the RVA might be the most biologically useful approach of the many approaches to hydrological classification that employ ecologically relevant flow indices (Section 4.1). Indeed, Poff *et al.* (2006a) found that the IHA variables adequately represented the majority of flow variation explained by a larger group of 171 flow indices.

Critique

Most hydrological methodologies produce rapid and non resource intensive, but also simplistic, inflexible and low resolution environmental flow estimates (Tharme 1996, 2003; Petts *et al.* 1996; Arthington *et al.* 2006). They therefore remain most appropriate at the scoping or planning level of water resource development for conservative allocation of water for the ecosystem, where environmental flow regionalisation is required by river ecotype, or in low controversy situations where they may be used to derive preliminary flow management targets (e.g. Caissie and El-Jabi 1995). They have also been used by engineers to determine simple operating rules for dams or off-take structures where few or no local ecological data are available (Acreman and King 2003).

The vast majority of hydrology-based methods fail to adequately address the dynamic nature of the flow regime, with little attention to flow timing or ecologically important flow events (Tharme 1996; Richter *et al.*

1997a; Arthington and Zalucki 1998a; Bragg *et al.* 1999; Annear *et al.* 2004). Moreover, they tend not to explicitly include ecological data, rendering them of questionable ecological relevance (Tharme 1996, 2003; Arthington *et al*. 2006). Arthington and Pusey (2003) and Arthington *et al*. (2006) cautioned against such routine reliance in river management on simplistic, static environmental flow rules purported to associate degrees of flow modification with plausible ecological outcomes, but typically largely without a substantiated empirical basis. They considered such approaches liable to contribute to further ecosystem degradation, and risk undermining previous work aimed at developing the scientific foundation of environmental flow assessment. Though not without the kinds of limitations outlined in Mathews and Richter (2007), advancements in RVA and similar methods were developed to redress such issues.

1.5.4 Hydraulic rating methodologies

From the 1970s onwards, initially in North America and alongside hydrological approaches, there was rapid development of methodologies that examined, for the first time, the effects of specific discharge increments on instream physical habitat, for fish maintenance, passage, spawning, rearing and other flow-related requirements and utilised the quantified habitat-discharge relationship(s) to determine environmental flows (Stalnaker and Arnette 1976; Prewitt and Carlson 1980; Newcombe 1981; Gordon *et al.* 1992; Tharme 1996). Pioneers of the approach included Collings *et al.* (1972, cited in Trihey and Stalnaker 1985) and Waters (1976). Two groups of transect-based methodologies evolved from these foundations, hydraulic rating and habitat rating approaches (Stalnaker 1979; Trihey and Stalnaker 1985; Richardson 1986), with the latter group using hydraulic data collected at multiple cross-channel transects or throughout a study reach (Section 1.5.5).

Basis and extent of application

Loar *et al.* (1986) coined the term 'hydraulic rating' methodologies for approaches that use changes in simple hydraulic variables, such as wetted perimeter or maximum depth, usually measured across single, limiting river cross-sections (typically riffles), as a surrogate for habitat factors known or assumed to be limiting to target biota (Section 6.1). The assumption implicit in such approaches is that ensuring some threshold value of the selected hydraulic parameter at altered flows will maintain the biota and/or ecosystem integrity (Tharme 1996). Commonly, a breakpoint on a plot of the variable of concern against discharge, interpreted as a threshold below which habitat quality becomes significantly degraded, is identified on the response curve as the recommended environmental flow, or it is set as the discharge producing a fixed percentage reduction in habitat (Gippel and Stewardson 1998).

Of 23 hydraulic rating methodologies reported in the literature (11% of the global total - Figure 1.5), most were developed in North America during the 1960s-1970s to recommend flows to maintain economically important salmonid fisheries (Stalnaker and Arnette 1976; Tharme 1996) and have been superseded by habitat simulation methods (Tharme 2003). By far the most commonly applied hydraulic rating

methodology worldwide today, and already the third most used approach in North America more than a decade ago (Reiser *et al.* 1989b), is the generic Wetted Perimeter (WP) method (Tharme 2003).

In the WP method, it is firstly assumed that river integrity can be directly related to the quantity of wetted perimeter, typically in riffles or other critically limiting habitats, and secondly that preservation of such areas will ensure adequate habitat protection overall. An established empirical or hydraulically modelled relationship between wetted perimeter and discharge (Q) is used to determine minimum or preservation flows, usually for fish rearing or maximum production by benthic invertebrates (e.g. Nelson 1980; Richardson 1986; Brizga 1998; Chapter 6). The recommended flow is either identified from discharges near the curve breakpoint, which is presumed to represent optimal conditions and below which habitat is rapidly lost (Stalnaker *et al.* 1994; Gippel and Stewardson 1998; Espegren 1998), or as an allowable percentage habitat retention (Bragg *et al.* 2005; e.g. a 25% reduction in WP from that at average discharge). Riffle WP-Q relationships have been employed to identify environmental flows to maintain or optimize benthic invertebrate productivity or diversity, based upon the premise that riffles are the most productive or biologically diverse habitat patches (Gore 1989; Tharme 1996). A detailed Australian application and evaluation of the method is provided in Gippel and Stewardson (1998).

Critique

Hydraulic rating methodologies are reliant on the simplistic assumption that a single hydraulic variable can adequately represent the flow needs of a target species for a particular activity, and by inference, with placement of the single cross-section critical to the results obtained (Tharme 1996). Moreover, the general approach cannot readily be used for certain riverine ecosystem components (e.g. riparian vegetation). Although the outputs are of fairly low resolution, hydraulic rating methodologies allow a rapid, focused and flexible flow assessment for one or a few assemblages, species or activities, and for the maintenance of habitat area for requirements such as invertebrate production. Tharme (1996) and Dunbar *et al*. (1998) considered these methodologies precursors of more sophisticated habitat simulation methodologies. Although it is probable that the WP method, in particular, will continue to be applied, it most likely will be applied as one of a set of methods utilized within holistic approaches (Tharme 2003).

1.5.5 Habitat simulation methodologies

Basis and extent of application

In habitat simulation methodologies, modelling analyses of the quantity and suitability of instream physical habitat available to target riverine biota under different hydrographs, using integrated hydrological, hydraulic and biological response data, are used to identify appropriate environmental flows (Loar *et al.* 1986; Herricks and Braga 1987; O'Keeffe *et al.* 1989b; Tharme 1996, 2003; Palau and Alcazar 1996; Acreman and Dunbar 2004). Habitat simulation approaches generally are underlain by the fundamental assumption that hydraulic habitat (Section 1.4.8) is a determinant of the distribution and abundance of aquatic biota, with species

exhibiting preferences (optima) within the range of conditions that they can tolerate, and that these ranges can be defined and the area providing these conditions quantified as a function of discharge (Bovee 1982).

Habitat simulation methodologies ranked second only to hydrological methodologies in terms of use, at 28% of the global total (Figure 1.5), with approximately 58 recorded from different countries (Tharme 2003). Of this number, roughly half represent *ad hoc* approaches that are no longer applied (e.g. Oregon Usable Width Method; see Stalnaker and Arnette 1976). A subset of techniques representing the current state-of-the art, evolved from these earlier approaches, however, including IFIM (Section 1.1.3) and a suite of more recent habitat simulation models of similar character (see below).

The IFIM, including its cornerstone, the Physical Habitat Simulation Model, PHABSIM, was initially devised by the then Co-operative Instream Flow Service Group of the US Fish and Wildlife Service (USFWS), Colorado, in the late 1970s (Reiser *et al.* 1989b). It remains considered by many practitioners as the most scientifically defensible methodology available for assessing environmental flows (Shirvell 1986; Gore and Nestler 1988; Dunbar *et al.* 1998; Tharme 2003). It comprises an array of over 240 hydraulic and habitat simulation models (Bovee 1982; Milhous e*t al.* 1989; Nestler *et al.* 1989; Stalnaker e*t al.* 1994; Stalnaker 1998). In combination, these models integrate predicted changes in habitat (as Weighted Usable Area, WUA), with the preferred hydraulic habitat conditions for target species life stages or assemblages, and for particular activities (e.g. migration, spawning), often depicted using habitat suitability index (HSI) curves (e.g. Bovee and Cochnauer 1977; Bovee and Zuboy 1988), at discharges of interest. Microhabitat is most commonly defined by depth, average velocity, substratum composition and cover (Bovee 1982; Orth 1987), though more complex hydraulic indices are also examined (e.g. Souchon and Capra 2004). The resultant habitat-discharge outputs, often depicted as effective habitat time series and/or duration curves for different flow regimes, are used to predict the optimum flows to meet a particular environmental flow objective or to evaluate alternative flow regulation scenarios (e.g. Bovee 1982; Orth and Maughan 1982; Annear and Conder 1984; Gore 1989; Alves *et al.* 1996; Waddle 1998a, b).

Most frequently, IFIM has addressed the flow requirements of fish species (Orth and Maughan 1982; Loar *et al*. 1986; King and Tharme 1994; Stalnaker *et al.* 1996). It has increasingly been applied for invertebrate taxa, however, to the extent that it is the most common method by which discharge, hydraulic habitat and invertebrate response are linked in environmental flow determinations or used predictively to assess flow-related changes in benthic distribution patterns (e.g. Orth 1987; Gore and Nestler 1988; Campbell 1991, 1992; Tharme 1996; Tharme and King 1998; Gore 1987, 1998; Choy 1998; Petts *et al*. 1999; Jowett 2003; see also Section 8.1). The IFIM remains by far the most commonly used environmental flow methodology in North America (Reiser e*t al.* 1989b; Armour and Taylor 1991; Annear *et al.* 2004; but see Section 1.5.6) and applications of the methodology elsewhere have continued to expand (e.g. Leclerc *et al.* 1995; Alves *et al.* 1996; Viganò *et al.* 1997; Stalnaker 1998; Blažková *et al*. 1998; Gustard and Elliott 1998; Nakamura

1999; Souchon and Capra 2004; pers. obs.). Tharme (2003) showed that its use far exceeded that of other methodologies of its type worldwide, with confirmed use in at least 20 countries at that time.

The German reach-based, Computer Aided Simulation Model for Instream Flow Requirements in regulated streams or CASIMIR (Jorde 1996; Jorde and Bratrich 1998; Jorde *et al.* 2001), was found to be the second most commonly applied habitat simulation methodology, after IFIM, reported in six countries, all but one in Europe (Tharme 2003). In the method, relationships between spatiotemporal patterns in benthic shear stress (Statzner and Higler 1986; Statzner *et al.* 1988), as a measure of habitat availability and quality, and different discharge regimes are described, linked to habitat suitability curves for invertebrates for shear stress (Jorde 1996; Jorde and Bratrich 1998). Other similar approaches based on hydrological, hydraulic and habitat simulation modelling include the Norwegian River System Simulator (RSS; Alfredsen 1998), the French Evaluation of Habitat Method (EVHA; Ginot 1995); the New Zealand River Hydraulics and Habitat Simulation Program (RHYHABSIM; Jowett 1989); MesoHABSIM (Annear *et al.* 2004); the Canadian microhabitat modelling system, HABIOSIM (Dunbar *et al.* 1998); and the Riverine Community Habitat Assessment and Restoration Concept (RCHARC, Nestler *et al.* 1996; Richter *et al.* 1997a).

Critique

Habitat simulation techniques are deemed more suitable than hydrological or hydraulic rating methodologies in high profile cases, for rivers of exceptional conservation importance, or where negotiated decisions on water allocations are made (Lamb 1989). The reason being they provide consistently applied assessments of changes in physical habitat with discharge at a scale that is relevant to the biota and allow comparisons to be made of the flow needs of single or multiple species, life stages and assemblages under various flow scenarios (Prewitt and Carlson 1980; Tharme 1996; Dunbar *et al.* 1998). Where the aim is to maintain a healthy whole riverine ecosystem rather that target organisms, or in cases where there is a paucity of knowledge on the biological requirements of riverine species, however, holistic type methodologies are liable to be more appropriate (King and Tharme 1994; Tharme 2003; Section 1.5.6).

The structured processes of data collection facilitate investigation of the relationships between flow-related hydraulic habitat and invertebrate (and other aquatic biota) distribution patterns, for example by means of HSI curves, enabling determination of the low (and high) flow requirements of riverine invertebrates, fish and other biota. Moreover, the models enable efficient processing of large amounts of data and often have sophisticated hydrological and habitat-response time series components, as well as outputs at a high degree of spatial and temporal resolution (Tharme 1996). The methodologies perform best when the habitat requirements of the modelled species at different life stages are known (Richter *et al.* 1997a).

There are several limitations and deficiencies inherent in habitat simulation methodologies (see Tharme 1996 for a full account), however, many of which have been expressed in reviews of specific methodologies, especially of IFIM. General critiques of IFIM (/PHABSIM) highlighting its problem areas as well as

strengths are particularly numerous given the methodology's status, and are provided in Mathur *et al.* (1985), Shirvell (1986), Scott and Shirvell (1987), Gore and Nestler (1988), Gan and McMahon (1990a, b), King and Tharme (1994), Tharme (1996), Gippel and Stewardson (1997), Jowett (1997), Arthington and Zalucki (1998a), Dunbar *et al.* (1998) and Souchon and Capra (2004).

A major shortfall of habitat simulation modelling in PHABSIM (Nestler *et al.* 1989) and similar approaches, is the single-species bias, with all its attendant problems (see Tharme 1996), as well as inadequate, reductionist treatment of complex ecosystem interactions and processes, resulting in limited realism of its biological assumptions and a lack of whole ecosystem understanding (cf. holistic methodologies, Section 1.5.6; Mathur *et al.* 1985; Shirvell 1986; Orth 1987; Scott and Shirvell 1987; Gore and Nestler 1988; Arthington and Pusey 1993; King and Tharme 1994; Castleberry *et al*. 1996; Richter *et al*. 1997a; Arthington and Zalucki 1998a). Moreover, management decisions based on environmental flow objectives focused on a limited number of species and their habitat requirements may actually result in undesirable effects on the entire ecosystem.

Habitat simulation models (e.g. PHABSIM) were found to provide limited representation of patterns of interaction between flow regime and channel morphology and long-term geomorphological change in rivers, as well as of ecological responses to flow alteration (King and Tharme 1994; Tharme 1996; Arthington and Zalucki 1998a). They also cannot be readily used as yet, for certain components of the riverine ecosystem, such as riparian vegetation. Although advances have been made in the links between the outputs from methodologies, such as IFIM, and both the historical hydrological regime and likely responses of invertebrates/other biota to flow disturbance, the outputs remain focused on changes in physical habitat area with discharge, with limited indication of which altered flows represent unacceptably high degrees of impact or of the ecological responses that might be expected.

The validity of the primary assumptions on which most methodologies are based, that species are mainly limited by the availability of suitable microhabitat, and that a small subset of hydraulic variables can adequately describe microhabitat for biota (Bovee 1986) are subjects of continued debate (Sections 1.4.8 and 8.1). Constraints to proper implementation of approaches such as IFIM/PHABSIM have been revealed in terms of physical habitat characterization, including the construction and degree of transferability of HSI curves, often the most complex, time-consuming and costly aspect of application (Mathur *et al.* 1985; Shirvell 1986; Gore and Nestler 1988; Reiser *et al.* 1989; Gan and McMahon 1990a, b; King and Tharme 1994; Bovee 1996). Although depiction of the flow-related habitat needs of a broad range of species and diverse life cycle activities is highly flexible using HSI or similar curves, there are potential sources of error and biases associated with curve development and application (Prewitt and Carlson 1980; Bovee 1986; Shirvell 1986). It is now well recognised, for instance, that curves compiled from species microhabitat data for various reaches of the same river, for different seasons, or for the same species for different rivers, may be highly divergent (e.g. Gan and McMahon 1990a; Groshens and Orth 1994). Moreover, suitability criteria

are essentially empirical correlations which provide limited insight into biological processes or the reasons why certain habitat conditions are preferred. The consensus nowadays, therefore, is that it is inappropriate to use hydraulic habitat suitability curves with populations, activities, and environs other than the ones from which they were derived.

Earlier versions of habitat simulation methodologies were particularly deficient in having models that proved complex to run, yet produced oversimplified representations of hydraulic habitat (but cf. Estimhab as an alternative to PHABSIM; Souchon and Capra 2004), with high associated error margins, difficulties in calibration and limited extrapolation possible outside measured discharge ranges (Bovee and Milhous 1978; Mathur *et al.* 1985; Shirvell 1986; Scott and Shirvell 1987; Gan and McMahon 1990a, b; King and Tharme 1994; Leclerc *et al.* 1995; Waddle 1998b). Such models also could not easily simulate certain flow-habitat conditions, for example, instances where areas of river bed were frequently uncovered at low discharges. Increasing effort has been directed at expanding the range and complexity of hydraulic habitats modelled, so as to more accurately reflect the hydraulic conditions that are experienced by the biota and of multiple river types (Stalnaker *et al.* 1994; Ghanem *et al*. 1996; Blažková *et al*. 1998; Souchon and Capra 2004). There has been a move towards increasingly high degrees of spatial and temporal resolution as advancements are made in two- and three-dimensional hydraulic habitat modelling, with treatment of the river reach as a spatial continuum (rather than on the basis of independent cross-sections), as well as the inclusion of more spatially explicit habitat metrics (e.g. Leclerc *et al.* 1995; Bovee 1996; Hardy 1998; Alfredsen *et al*. 1997; Waddle 1998b; Ghanem *et al.* 1996; Blažková *et al*. 1998; Parasiewicz and Dunbar 2001; Crowder and Diplas 2000; Lamouroux and Souchon 2002). Such modelling has shown potential for new and more accurate, quantitative representation of habitat-flow spatial and temporal patterns for aquatic biota than earlier one-dimensional approaches, and often with fewer data demands. Waddle (1998b) discussed the importance of various spatially explicit habitat metrics (e.g. a contagion index for juxtaposition of habitat patch types), with a view to their ultimate incorporation in instream flow (IFIM) habitat modelling.

With progress in ecohydraulics (Section 1.4.8), the focus on the types of hydraulic habitat variables of relevance to instream flow studies has shifted over the past 15 years to include a combination of standard variables (e.g. depth, velocity) with more complex integrated hydraulic indices (e.g. shear stress, as in CASIMIR) considered more influential in shaping physical microhabitat at the substratum-flow interface for benthic macroinvertebrates and fish and, hence, more realistic descriptors of the actual hydraulic conditions experienced (Statzner and Higler 1986; Statzner *et al*. 1988; Gore and Nestler 1988; Cheslak and Jacobsen 1990; Stalnaker *et al.* 1994; Gore 1996; Annear *et al*. 2004; Souchon and Capra 2004). In addition, habitat models have been expanded over time to include additional variables, for application at the biotope level (e.g. Modde and Hardy 1992), at community or guild level with statistical hydraulic models linked with multivariate habitat use models (e.g. Bain *et al.* 1988; Lamouroux *et al.* 1998, 1999; Lamouroux and Souchon 2002), and with links to population response models to increase the potential for ecological prediction (e.g. for IFIM/PHABSIM: Williamson *et al.* 1993; Nehring and Anderson 1993).

Significantly, habitat simulation techniques are increasingly used as one of a typology of tools (Souchon and Capra 2004), often within holistic methodologies (next section), due to the kinds of strengths and limitations outlined above (Tharme 2003).

1.5.6 Holistic methodologies based on functional analysis of hydrology-ecology relationships

Early reviewers recognised only the above three methodology types (Sections 1.5.3-1.5.5), while the emergence of a fourth type, 'holistic' (*sensu* Tharme 1996) or functional analysis methodologies, was first documented in Arthington *et al.* (1992) and is explicitly considered in most subsequent reviews (e.g. Petts and Maddock 1994; Tharme 1996, 2003; Stewardson and Gippel 1997; Arthington 1998a; King *et al.* 1999); prior to the early 1990s, there were no formally recognised or standardised holistic flow methodologies in place.

An ecosystems approach to river management had been advocated by freshwater ecologists for two decades (Ward and Stanford 1987; Petts 1989, 1996; Hill *et al.* 1991; Poff *et al.* 1997) and is since heralded as one of the chief directions of evolution of environmental flow science (Arthington *et al.* 1992; King and Tharme 1994; Richter *et al.* 1996; Dunbar *et al.* 1998; Tharme 2003). Indeed, Arthington (1998a) stated that from a global perspective there did not appear to be any competing paradigm for environmental flow assessment. The majority of environmental flow methodologies, although potentially useful for calculating the flow needs of individual species/assemblages, have been criticised for their simplistic treatment of the complexity of ecosystem interactions and processes (e.g. Arthington and Pusey 1993; King and Tharme 1994; Arthington *et al*. 2006; Section 1.5.5). Moreover, Richter *et al*. (1997a) observed that advances in understanding of the relationships between river ecological integrity and hydrology had borne limited influence on environmental flow determination thus far, with the potential use of long-term streamflow data and statistical descriptions of natural flow variability to set ecosystem-based management targets underutilized or neglected.

Holistic methodologies have set promising trends towards more integrated analyses of new knowledge on ecology-hydrology relationships in environmental flow assessment (Arthington 1998a; Tharme 2003; Poff *et al.* 2010; Chapter 9), while water management infrastructure provides ideal opportunities nowadays for testing, within an adaptive management framework, the extent to which hypothesized ecological outcomes of flow restoration are realized (Poff *et al.* 2003; Richter *et al.* 2006).

Methodology basis and extent of application

Holistic methodologies emerged from the common conceptual origin and guiding principles articulated in Section 1.1.3 and Arthington *et al.* (1992), as well as a grounding in stream ecosystem theory (Section 1.4), to form a distinct group of approaches focused from the outset towards addressing the environmental flow

requirements of the entire riverine ecosystem (Arthington *et al.* 1992; Growns and Kotlash 1994; Petts *et al.* 1995; Tharme 1996; Tharme and King 1998; Arthington 1998a; Pusey 1998; Dunbar *et al.* 1998; King *et al.* 1999; O'Keeffe 2000; Postel and Richter 2003; Schofield *et al.* 2003; Arthington *et al.* 2004).

Such environmental flow approaches that meld applied river management and current ecological theory based on knowledge of the relationships between hydrological variability and ecology, including predictive river-specific models, are uncommon yet essential for effective river conservation (Karim *et al*. 1995; Richter *et al*. 1997a; Arthington and Pusey 2003). They are reliant for their success on the well established body of interdisciplinary knowledge of the flow-related conditions governing various aspects of river ecosystem structure and functioning and under which riverine biota exist, and of the potential impacts of altered flow patterns on these (Section 1.3). This knowledge base provides an indication of which flows within the river's hydrological regime might be considered more relevant than others for ecosystem maintenance. It is implicit that the flow attributes incorporated in the modified, environmental flow regime fall within the range of values that characterize the historical, natural pattern, with a recommended flow regime assumed ecologically unacceptable if it contained flow elements that had never occurred in the natural regime (Pusey 1998). Thus, a central aim of an holistic environmental flow determination perhaps should be to identify and avoid breaching thresholds of flow regime alteration that might result in critical shifts in ecosystem state, particularly from a natural pre-disturbance regime to a less desirable one (Arthington 1998a).

Although representing at least 8% of the global total (Figure 1.5), but with more than 16 methodologies applied in Australia, South Africa, the U.K. and U.S.A., holistic EFMs have contributed greatly to the field of environmental flow assessment in recent years (Tharme 2003). Additionally, several other methodologies that are less well known contain holistic elements (see Tharme (2003) for discussion). Centred in Australia and South Africa (Section 1.1) where the emphasis is on ensuring the protection of entire rivers and their often poorly known biota, they rapidly took precedence over habitat simulation methodologies. Holistic methodologies have also stimulated considerable interest in developing world regions where environmental flow research is in its infancy and water allocations for ecosystems must, for the time being at least, be based on scant data, best professional judgement and risk assessment.

In an holistic approach, those flow events believed to be most important are identified from a statistical characterization of flow regime attributes, for some or all major biophysical components or attributes of the riverine ecosystem. This is done either through a prescriptive (bottom-up) or, more common recently, an interactive (top-down or combined) scenario-based, process that requires considerable interdisciplinary expertise and knowledge (Tharme 1996, 2003; Tharme and King 1998; Arthington 1998a; King *et al.* 2003; Arthington *et al*. 2004). The basis of most methodologies is the systematic construction of a modified flow regime on an element-by-element basis, where each element represents a well defined feature of the flow regime intended to achieve particular ecological, geomorphological and/or social objectives in time and

space. In contrast, in scenario-based approaches, environmental flows are defined in terms of the biophysical (and social) implications of various degrees of departure from the reference flow regime (King *et al.* 2003), under different development scenarios, rendering them less susceptible to omission of critical flow features than their bottom-up counterparts (Bunn 1998).

The BBM (King and Tharme 1994; Tharme and King 1998; King and Louw 1998; King *et al.* 2000) and Holistic Approach (Arthington 1998a) developed independently in South Africa and Australia, respectively, from the common conceptual framework established in late 1991 (Arthington *et al.* 1992). Together they provided the impetus and foundation for the rapid establishment within only a decade of most other methodologies of this type (Tharme 2003). In the BBM, an assessment is made of site-specific flow-ecology relationships, with a strong, but not necessarily exclusive, dependence on established links between flow regime characteristics and physical habitat or life history attributes. The basic output from the BBM, a tabulation of low to high flow requirements, with biophysical motivations, by month of the year, is generated for both maintenance (normal) and drought conditions (King and Louw 1998; King *et al.* 2000). The required environmental flows can be translated into representative time series of reservoir flow releases using an operating rule model (Hughes *et al.* 1997; Hughes and Ziervogel 1998), as well as percentage assurance rules for supply, for integration with the assurance levels of other water uses, using water resources yield modelling (Hughes 1999, 2001; Hughes and Münster 2000). The analysis of flow scenarios generated in this manner, as well as the establishment and implementation of a monitoring protocol for the recommended flow regime, to ascertain whether or not environmental flow objectives have been achieved, are also aspects of the methodology (King *et al.* 2000).

The BBM is presently the most frequently applied holistic environmental flow methodology in the world (Tharme 2003). In modified forms (i.e. Intermediate and Comprehensive Determination methods; DWAF 1999a, b) it represents the established methodology for routine determination of the ecological Reserve, having been applied in over 97 assessments of South African rivers by 2003 (Hughes and Hannart 2003). It has also been applied in Australia (e.g. Arthington and Lloyd 1998). Several ecological Reserve applications have incorporated the Flow Stressor-Response (FSR) method developed by O'Keeffe *et al*. (2002), which uses relationships between low and high flows and corresponding ecological stresses to generate time series of stress indices, linked to a river's flow regime (Section 8.1). These stress regimes allow for the evaluation of the ecological consequences of a range of flow scenarios, each with expression of the potential risk of change in river ecological condition. Hughes and Hannart (2003) recognised that the FSR method and Downstream Response to Imposed Flow Transformations (DRIFT; below) have the potential to provide options on how ecological functioning and flow-habitat relationships can be built into the Desktop Reserve model (Section 1.5.3) to enhance its ecological relevance.

The DRIFT process evolved from the BBM as an holistic, interactive data management system comprised of biophysical, social, scenario development and economic modules (Brown and King 2000; King *et al.* 2003;

Brown and Joubert 2003). It focuses on identification, by a multidisciplinary team, of the consequences of reducing river discharges from natural, through a series of flow bands associated with particular sets of biophysical functions, and of specific hydrological and hydraulic character, in terms of ecosystem response. Brown and Joubert (2003) described the use of multicriteria analysis by which the environmental flow scenarios are established for comparative evaluation of their respective biophysical and socioeconomic consequences. In DRIFT, links between social consequences for subsistence users, which are evaluated alongside ecological and geomorphological ones, and economic implications in terms of mitigation and compensation, are explicit and comprehensive. A number of methods combining elements of the BBM and DRIFT, simplified to deal with resource constraints, have been applied in developing countries with varying success (see Tharme (2003) for examples).

A diverse range of holistic EFMs has been developed in Australia (Arthington 1998a), many adopting a multidisciplinary expert panel process (Cottingham *et al*. 2002) similar to that of the BBM and DRIFT. Examples include the Expert Panel Assessment Method (Swales *et al.* 1994; Swales and Harris 1995), Scientific Panel Assessment Method (SPAM; Thoms *et al.* 1996), and various other expert-based approaches (e.g. Gippel *et al.* 1994; Cottingham *et al*. 2001). Other holistic methodologies that have emerged in recent years in Australia include: the Flow Restoration Methodology, FLOWRESM (Arthington 1998b; Arthington *et al*. 2000), aimed specifically at addressing environmental flows in river systems exhibiting a long history of flow regulation and requiring restoration; the Flow Events method, which characterizes environmental flows on the basis of knowledge of the influences of several specific flow events on ecological and geomorphological processes (e.g. frequency analysis of minimum WP-Q relationships; Stewardson and Gippel 2003); and the Benchmarking methodology, an appropriate approach for making probability statements regarding the ecological implications and risks (for all major ecosystem components) of altering the hydrological regime of a river to different degrees, as compared with the natural regime, at basin scale (Arthington 1998a; Arthington and Pusey 2003; Arthington *et al*. 2004).

Similar approaches are evolving within adaptive management frameworks, where environmental flow targets or rules are set based on natural flow regime variability, available hydroecological understanding and expert judgement, and then validated through monitoring, to establish river-specific benchmarks for ecological condition (e.g. Baron *et al.* 2002; Richter *et al.* 2003, 2006). Arthington *et al*. (2006) proposed such an approach that endeavours to bridge the gap between simple hydrology-based methods (Section 1.5.3) and more comprehensive, river-specific holistic approaches, particularly for instances where site-specific hydrological and biological data are non-existent or liable to remain limited. Regional environmental flow standards are established that incorporate ecologically relevant attributes of natural flow variability common to classes of hydrologically similar rivers, based on generic flow-ecological response relationships for each of a number of ecological health metrics, across a gradient of flow alteration, for individual flow variables and river classes (Arthington *et al*. 2006, p. 1314, Figure 1). The general approach has been extended as a

new regional framework for environmental flow assessment, currently under trial, the Ecological Limits of Hydrologic Alteration (ELOHA; Poff *et al.* 2010).

The River Babingley (Wissey) Method, developed in England (Petts 1996; Petts *et al.* 1999), represents one of few holistic methodologies developed or applied outside Australia and South Africa (Tharme 2003). Richter *et al*. (2006) provide another, in the form of a five-step adaptive, interdisciplinary science-based process for environmental flows developed first on the Savannah River, U.S.A., that represents the dominant holistic approach routinely applied to date in North America; Postel and Richter (2003) give further examples for U.S. rivers.

Critique

Various methodology-specific critiques, as well as research and development requirements for holistic methodologies, are provided in, among others, Tharme (1996, 2003), Arthington (1998a), Arthington *et al.* (1998b, 2004), Dunbar *et al*. (1998), King *et al.* (1999), Cottingham *et al*. (2002) and Schofield *et al.* (2003).

Holistic methodologies exhibit several advantages over other types of environmental flow methodology, most importantly perhaps in that they can potentially be used to address all components of the riverine ecosystem, in an integrated fashion, and have clear, well developed links with natural hydrological variability and regime characteristics (Section 1.4). They are able to consider all elements of the flow regime, such as the magnitude and timing of both low flow and flood events, and their outputs can be generated at several levels of resolution. Hence, they are pragmatic, flexible and robust, and can be adapted to cope with situations where time, available data and expertise are constraints. In most instances, the environmental flow strategies generated in holistic assessments are based on the best available, multidisciplinary scientific understanding of riverine ecology and effectively utilize a wide range of existing knowledge (Arthington 1998a; Tharme 2003). As they rely to a considerable extent on professional judgement, care must be taken to apply them in a rigorous, structured manner, to ensure scientifically and legally defensible results.

Holistic methodologies are fundamentally dependent on knowledge of the natural hydrological regime as a guide to which flow events to address. Consequently, they are reliant on high quality data from daily hydrological models and are affected by model limitations. Considerable effort is required to advance the accuracy and applicability of hydrological models under various flow conditions. In addition, the models need to address more effectively the effects of changes in land use and other factors on river hydrology (Arthington and Zalucki 1998b; Poff *et al*. 2006b).

Importantly, holistic approaches also tend to be reliant on quantitative flow-ecology modelling, as they must if they are to possess the predictive capabilities increasingly required in environmental flow assessments nowadays (Tharme and King 1998; Arthington *et al.* 1998b; Dunbar and Acreman 2001; Bunn and

Arthington 2000). The methodologies therefore need to build upon and/or be frequently evaluated in the light of ongoing advances in ecohydrology, including ecohydraulics (Sections 1.4.1 and 1.5.8). The more advanced holistic methodologies routinely utilise several of the tools for hydrological, hydraulic and physical habitat analysis featured in the other methodology types, within a data management framework, for establishing environmental flows (Tharme 2003). Although detailed physical habitat and water quality modelling are not routinely performed in holistic methodologies to date, there is scope for greater incorporation of such tools.

Arthington *et al*. (1998a), Brizga (1998) and Tharme (2003) observed that bottom-up holistic EFMs are likely to continue to be applied most commonly in the near future, but suggested that the most rigorous approach would be a combined bottom-up/top-down approach, along the lines proposed in Arthington *et al*. (2006). Greater attention needs to be given to monitoring and targeted additional ecohydrological research for refinement of flow recommendations and the overall adaptive management strategy (Richter *et al*. 2003; Poff *et al*. 2003). Such feedback is essential, given the constraints imposed by limited scientific data and the tremendous reliance on expert judgement.

There are few applications of holistic methodologies other than in their place of origin, and mostly only local critiques are provided in the literature. Moreover, as holistic methodologies comprise a recent area of environmental flow science, they all require comparison with other international methodologies, explicit testing and verification of their assumptions, and assessments of their sensitivity, reproducibility and predictive capacity.

2. STUDY AREA AND PILOT SURVEY FOR SITE SELECTION

2.1 DESCRIPTION OF THE GENERAL STUDY AREA

The study area is within the southwestern region of the Western Cape Province, South Africa, the general features of which are described below. It encompasses the area within which the pilot survey was conducted (Sections 2.2 and 2.3) and hence, the catchments of the rivers on which sites were selected for the detailed low flow study (Elands, Molenaars, Du Toits and Riviersonderend; Section 2.4) – the 'core study area'.

2.1.1 Climate and hydrology

The southwestern Cape represents one of the more mesic regions of South Africa (Section 1.1.1), possessing a Mediterranean climate characterized by cool winters with moderate to high precipitation and dry, hot and windy summers (Allanson *et al.* 1990; Davies and Day 1998). The study area falls within the winter rainfall region (Dyer 1976), with roughly 80% of precipitation occurring between April and September (DWAF 1994), from a combination of orographic effects and cold fronts approaching from the southwest. Mean annual precipitation (MAP) is high and spatially variable, being influenced considerably by local topography. The overall MAP range for the southwestern Cape is 200-1500 mm y^{-1} (WR90 map, updated by IWQS in 1998; Dent *et al.* 1989). It can reach a maximum of *c.* 2600 mm y^{-1} in the high-lying, western part of the study area (which encompasses the main study sites - Section 2.4), while values in the southeastern coastal area are *c.* 600 mm y^{-1} (Everett and Quibell 1995; DWAF 1994, 1997). During the dry months, precipitation is usually in the order of only 126-250 mm a^{-1}, with isolated areas receiving 62.5-125 mm y^{-1} (Davies and Day 1998). Inter-annual rainfall variability is low (15-20%). Mean annual evaporation (MAE) is typically less variable than MAP, and ranges from about 1100 mm y^{-1} to a maximum of 1700 mm y^{-1} in the core study area (WR90 map, updated by Institute for Water Quality Studies, IWQS, in 1998; Midgeley *et al.* 1994; DWAF 1994, 1997). Seasonality in evaporation in the core study area is pronounced, with high summer values of 230-250 mm y^{-1} and low winter values of 40-50 mm y^{-1} (DWAF 1997). Mean annual temperature ranges are in the order of 10-20 °C (DWAF 1999b). August minimum land temperatures range from 6-17 °C, with cooler temperatures in the mountainous areas (Dent *et al.* 1989).

In terms of regional hydrology, the southwestern Cape is dominated by two major river systems, the Berg and Breede (Midgeley *et al.* 1994). The catchment of the Breede contributes 4.2% to the total mean annual runoff (MAR) of South Africa, while the Berg River and other parts of the southwestern Cape together contribute a further 4.0% (King *et al.* 1979; DWA 1986). Mean annual runoff ranges from about 40 mm to as high as 1250 mm (Midgeley *et al.* 1994). The study area is within the geographically distinct 'winter peak

flow' region, with a marked seasonal distribution of flow into summer low flows and winter high flows (Joubert and Hurly 1994). The 'winter moderate' group of rivers (which includes all the study rivers; Section 2.4) typically exhibits highest monthly volumes during July and August (Figure 2.1; Section 2.3). Department of Water Affairs and Forestry drainage region H, which represents the Breede River catchment (and includes the four finalised sites) has a coefficient of variation (CV) of precipitation of 0.20-0.25, variable runoff CV of 0.26-0.72, and rainfall: runoff ratio of 20.2 (King and Tharme 1994). The study area falls within one of the five limnological regions of southern Africa, the 'temperate, acid waters of the Cape Fold Region' (Allanson *et al.* 1990). It is also part of the 'Cape system' hydrobiological region (Harrison 1965).

2.1.2 Geology, fluvial geomorphology and topography

The study area is largely within the Cape Folded Belt Geomorphic Province, which is bordered either side by the Southern Coast Geomorphic Province (IWQS map, updated in 1997; King 1963). Geologically, the southwestern Cape is dominated by the sedimentary strata of the Cape Supergroup, namely the Table Mountain Group/Series, TMS), Bokkeveld Group and Witteberg Group, in order of decreasing age (Lambrechts 1979; Moon and Dardis 1992). These strata overlay the older (550 Ma) Cape Granite Suite. There are also localised areas of Quaternary sediments (Moon and Dardis 1992). The mountains of the study area typically comprise resistant, well-leached TMS sandstones and quartzites (500-320 Ma) (Lambrechts 1979), as well as some younger Karoo Supergroup sediments (265-190 Ma; Davies and Day 1998). Erosivity is predominantly low to medium, with few areas of high potential erosion (ENPAT 97 map, DEAT 1997).

Broad terrain patterns ranging from plains to mountains correspond with recognised geomorphic provinces, and comprise the Coast Forelands and Cape Fold Region (ENPAT97 broad terrain patterns map, Department of Environment Affairs and Tourism, DEAT, 1997). Topographically, most of the southwestern Cape is less than 500 m in altitude, with flat lower river valleys (Davies and Day 1998). The source areas and upper catchments of the region's major river systems, in contrast, occur in mountainous terrain, at altitudes up to about 2000 m a.m.s.l. (Everett and Quibell 1995).

Southwestern Cape rivers tend to be short and fairly steep (King *et al.* 1979), with few extensive, long systems. However, the main geomorphological (and corresponding biological zones) identified for South African rivers are usually present (Harrison 1965; Noble and Hemens 1978; Rowntree and Wadeson 1999). These comprise the upper reach mountain headwall, mountain stream and foothill (and sometimes transitional) zones, as well as the lower reach transitional and lowland zones (described in Rowntree and Wadeson, 1999).

2.1.3 Catchment and riparian vegetation

The southwestern Cape is located within the Cape Floristic Region (CFR), the smallest and most geographically localised of the world's six floral regions, as well as a global epicentre of biodiversity, due to its exceptional species diversity and endemism (Bond and Goldblatt 1984; Cowling 1992; Cowling and Holmes 1992). Fynbos is the dominant vegetation type, contributing more than 80% of the region's species (Cowling and Richardson 1995; Davies *et al*. 1995), but substantial areas of karroid shrubland (Succulent Karoo Biome), Afromontane forest, renosterveld and subtropical thicket also occur (Low and Rebelo 1996). Fynbos, the most widespread of three shrubland vegetation types of the South African fynbos biome, comprises a complex association of fire-adapted sclerophyllous shrubs and heathlands of the Proteaceae, ericoids (including the dominant Ericaceae), geophytes and Restionaceae. It is uniquely characterised by the last family and is confined to the nutrient-poor soils of the southwestern and southern Cape (Specht and Moll 1983; Cowling and Richardson 1995).

The upper catchments of southwestern Cape rivers tend to be vegetated with mesic mountain fynbos and relatively undeveloped. Infestation by alien vegetation is, however, evident in these areas, while middle and lower catchments tend to be increasingly influenced by agriculture. Riparian vegetation within the study area is predominantly fynbos, but also includes elements of Afromontane forest, notably trees such as *Brabejum stellatifolium*, *Podocarpus*, *Olea* and *Rapanea* (Moll and Scott 1981; Hill Kaplan Scott, HKS, 1988; Cowling and Richardson 1995). Dominant alien riparian trees include *Acacia longifolia* (long-leaved wattle), *A. mearnsii* (black wattle) and *Sesbania punicea.* Several of the low-order mountain streams do not have a riparian canopy (Davies *et al*. 1995). *Prionium serratum* (palmiet) is a common streamside plant and the macrophyte, *Isolepis digitata*, also occurs in some rivers within the study area (Davies *et al.* 1993). Both plants are strongly linked to low-pH waters, particularly in upper catchments. There are no recorded alien macrophytes in the upper river reaches of the Breede System, although a non-indigenous moss might be present (C. Boucher, Botany Department, University of Stellenbosch, pers. comm.).

2.1.4 Water chemistry

The rivers of the southwestern Cape are characteristically oligotrophic, draining well-leached soils associated with TMS sandstones and quartzites (King *et al.* 1979). The pH also tends to be below neutrality, down to as low as 4.3, due to the nature of the soils and to high concentrations of humic (weak organic) acids released from fynbos (Davies *et al.* 1993). The naturally low buffering capacity of the region's rivers is a result of pH being determined largely by this vegetation type (Dallas and Day 1993). Salts of marine origin at lower altitudes variously influence the rivers, with a concomitant increase in buffering capacity to neutral pH (Davies *et al.* 1993). In terms of ionic dominance, the major ions of rivers within the study area tend to be Na^+ and $C\ell^-$ (King *et al.* 1992; Day and King 1995). The rivers have typically clear waters of low turbidity (and low total suspended sediments, TSS), and most sediment transportation occurs during the wet season in association with floods. Rivers in the region form two main groups (Harrison and Agnew 1962). The first

group are strongly acidic (pH 5.0-5.9) with unbuffered waters and low total dissolved solids (TDS), and are frequently peat-stained. The second group exhibit almost colourless waters, and a pH between 6.0 and 6.9.

A regional assessment by Dallas *et al.* (1998) encompassing the study area, of the background concentrations of system variables for least-impacted upper river sites, showed the following trends. Median values for mountain stream zones for TDS, conductivity, TSS and pH were: 26.3 mg ℓ^{-1}; 3.0 mS m^{-1}; 0.66 mg ℓ^{-1}; and 5.5 pH units, respectively. Similarly, corresponding median values for foothills were: 32.0 mg ℓ^{-1}; 3.1 mS m^{-1}; 0.78 mg ℓ^{-1}; and 6.0 pH units. Concentration ranges are given in Dallas *et al.* (1998). Similar data were not available for other variables.

2.1.5 Aquatic fauna

From a biotic perspective, the southwestern Cape represents one of ten South African biogeographic regions, the Capensis bioregion, delimited on the basis of select riverine flora and fauna at a secondary catchment scale (Eekhout *et al.* 1997). The Capensis bioregion is ajoined by the Karroid Capensis and Namaqua Capensis regions (and is also within the fynbos biome; Brown *et al.* 1996). On the basis of the above physiographic characteristics, the study area primarily encompasses the 'Cape folded mountains' ecoregion (Level I - DWAF 1999b).

Aquatic invertebrates are the dominant faunal component of southwestern Cape rivers. The communities include a high number of species endemic to the typically acidic, humic-stained rivers of the region (Harrison and Agnew 1962; Davies *et al.* 1993; Picker and Samways 1996). Some 64% of the freshwater invertebrate species of the CFR, representing almost one third of South African freshwater invertebrates, are endemic (Wishart and Day 2002). Insects typically constitute some 99% by number of the entire invertebrate community of the region's upper, low-order stony-bed rivers and streams (King 1981; this study). Dipterans tend to dominate, with Chironomidae and Simuliidae typically present (Davies *et al.* 1993), followed by Ephemeroptera, Plecoptera, Coleoptera, Trichoptera, Odonata and Megaloptera. Representatives of non-insect taxa, such as crustaceans, flatworms and oligochaetes are usually present in far lower numbers. Geomorphological river zonation (Section 2.1.2) is typically reflected in the invertebrate communities, with the mountain-stream zone generally inhabited by a slow-growing, insect-dominated community that is not strongly seasonally differentiated, except by developmental stage (King 1981). In contrast, foothill communities show distinct seasonal changes in species composition and abundance, with a roughly four-month summer and eight-month winter community.

The Cape component of the southern African temperate fish fauna comprises only 15 species, in the southwestern Cape restricted to the rivers of the Cape Fold Mountains (Skelton 1993). The distinct fauna is dominated by Cyprinidae, and also includes hardy common species such as *Galaxias zebratus* (Cape galaxias, Galaxiidae) and *Sandelia capensis* (Cape kurper, Anabantidae). Endemicity is highest in the southwestern Cape, which also includes the majority of threatened species (Skelton 1987, 1993).

Characteristically, only a few indigenous species occur in a single river and in low abundances, relative to the rest of the country. Several alien and translocated species occur in the southwestern Cape, *inter alia*, *Oncorhynchus mykiss* (rainbow trout) and *Salmo trutta* (brown trout) (Salmonidae), and the Centrarchidae, *Micropterus dolomieui* (smallmouth bass) and *Micropterus salmoides* (largemouth bass) (Skelton 1993).

2.2 SURVEY OF HYDROLOGICAL GAUGING WEIRS

2.2.1 Survey aim

Site selection first entailed a survey of hydrological gauging weirs on southwestern Cape rivers (Section 2.1) to locate suitable study sites for the low flow research outlined in Section 1.2. Rivers with hydrological gauging weirs on them, and for which a historical daily discharge record existed, were considered most suitable, as the flow record would provide information on the natural hydrological pattern of each river to which the riverine biotas had been responding in the long term (Chapter 4). Such knowledge was crucial, in that low flow events that constituted a physical disturbance in one river might be a natural feature of another. It was decided to limit the study to addressing the effects of low flows on upper reaches, as a different suite of effects would be expected to occur in middle or lower rivers, the majority of which are more heavily anthropogenically impacted. Consequently, only mountain stream to foothill zones were considered in the survey, as usually the least altered, and most diverse and disturbance-sensitive reaches (King *et al.* 1986). Originally, it was hoped to establish study sites on rivers where flow abstraction was occurring at a gauged diversion weir, and hence historically documented, so that there would be both an unimpacted reach upstream of the diversion weir and a downstream reach that had been subjected to the effects of flow reduction over a substantial time period, but this proved unachievable (Section 2.2.3).

2.2.2 Approach

A list was compiled of hydrological gauging weirs known on rivers throughout the southwestern Cape (DWA 1990), including diversion weirs and DWAF gauging weirs previously identified by Joubert and Hurly (1994) as recording near-natural flows (based on non-stationarity tests). It was circulated to DWAF personnel, Western Cape Region, as well as local researchers, for comment on the location of the weirs, their physical condition and age, accuracy, length and quality of the historical record, the physical character of the river reach on which they were situated, and any other potentially important information. A shortlist of 32 weirs was then compiled (Appendix 2.1), all of which were visited between January and February 1994. Site evaluation of the weirs and river reaches immediately above and below them was structured according to a set of predefined selection criteria (Table 2.1) aimed at minimising inter-system biological, geomorphological and hydrological variability.

Table 2.1 Selection criteria for use in the survey of rivers with DWAF hydrological gauging weirs.

- Long-term historical flow record: longer than 5 y.
- Average daily discharge data: data captured on computer and with the facility for updating the records to include the duration of the low flow experiment; gauge preferably still in operation.
- Accuracy of weir: moderate to high, and specifically suitable for measurement of low flows.
- Structure of the weir: preferably small size; limited upstream extent of effect of the weir pool.
- River zone: mountain stream, mountain stream-foothill transition, or foothill zone.
- Degree of anthropogenic disturbance: preferably zero to low disturbance; a high degree of naturalness (e.g. indigenous riparian vegetation).
- Position of reach locations[*1] and lengths: suitable physical character (see below); preferably one location upstream and one downstream of the weir, where both locations are representative of the same reach; short distances from each location to the weir, so that the discharge recorded at the weir reflects flow conditions within each location; locations at least 100 m long.
- Diversity of location hydraulic biotopes[*2]: riffles, runs and pools.
- Channel form and cross-section shape: natural or near-natural morphology.
- Substratum composition: predominantly cobbles and boulders.

- **For diversion weirs**: point abstraction at the weir; preferably no abstraction or water resource developments upstream of the weir; presence of gauge recording abstraction volumes.
- **For gauging weirs recording near-natural flow**: no abstraction of water or other form of flow regulation of the river system upstream of the weir.

[*1] Reaches were defined as geomorphologically relatively homogeneous sections of river less than 500 m long, while locations represented shorter sections of each reach (i.e. subreaches) of about 100 m long that appeared highly similar in character.

[*2] Hydraulic biotopes were recognised on the basis of surface flow type and substratum class (Chapter 3).

2.3 PILOT SURVEY OF BIOPHYSICAL CONDITIONS AT LOW FLOWS IN MULTIPLE RIVERS

2.3.1 Study objectives and approach

The main aim of the pilot survey was the identification of the most biophysically similar group of four rivers from the eight candidates identified during the gauging weir survey (Section 2.2), in terms of their abiotic character (hydrological regime, physical habitat, chemistry) and benthic macroinvertebrate assemblages, for use in a low-flow field experiment. Resh *et al*. (1988) recommended rivers selected for comparative disturbance studies be as similar as possible in hydrological regime and geomorphological character, while Fisher and Grimm (1991) acknowledged the different merits of using highly similar or disparate rivers.

The survey objectives were to:

1. Elucidate the relative similarities among the eight river sites in catchment conditions and broad hydrological regime, as well as physical habitat characteristics, water chemistry, and particularly benthic macroinvertebrate composition, under conditions of natural low flow (summer).
2. Assess the inherent biophysical variability within the reach represented by each site at low flows, based on comparisons of biophysical conditions at two locations within the same reach (approximating the

experimental control and impact locations used in the main study; Section 3.1.1).

3. Develop a preliminary understanding of relationships between invertebrate assemblage structure and environmental conditions during the dry season and hence, identify potentially useful physical habitat and chemical variables for inclusion in the main study.
4. Identify possible constraints to the interpretation of results from the planned comparative low flow experiment, when dealing with multiple rivers.

The eight pilot river sites are listed in Table 2.2, with their corresponding DWAF hydrological station numbers and locations. For each of the river reaches represented by the sites, two locations (i.e. short, similar reach sections) were chosen, less than 100 m apart. It was assumed that the planned diversions of flow for the main study would take place at the gauging weirs (but see Section 3.1). The two locations were positioned near the gauging weir, so that no tributary inflows or other significant discharge contributions to the mainstream occurred between each location and the weir. This ensured that the historical flow record (and hydrological data collected during the low flow experiment) was applicable to both of them, and that the experimental flow reductions could be effective in the case of the locations to be impacted.

It was the *a priori* intention to establish the future control location immediately upstream of the proposed flow diversion point, and the impact location at a location just downstream of it, but this was generally not possible. At the Du Toits site, both locations had to be located consecutively downstream of the gauging weir. This was due to the merging of a tributary with the mainstream a short distance upstream of the weir, so that there was too short a reach (< 50 m) for sampling purposes where recorded flows pertained to the mainstream. Moreover, the section appeared to be of less stable channel form. The two locations on the Hex River similarly were located downstream of the weir, as the area upstream was physically inadequate for sampling, due to a long pool/run reach. In the Riviersonderend reach, both locations were sited upstream of the weir, as the downstream reach was physically unsuitable after only *c.* 20 m, with a change to deep, palmiet-lined channels reflecting the uppermost extent of Theewaterskloof Reservoir. At Langrivier, the morphology of the reach downstream of the DWAF gauging station differed from that upstream, so both locations were located in the more homogeneous reach above the weir. At the Molenaars, Zachariashoek and Elands sites, two suitable locations were identified upstream of the gauging weirs, while at the Bakkerskloof site, a very short location was identified upstream of the weir, and a second, longer location was identified downstream of both the weir and a road culvert. A brief description of each site, with particular reference to the selection criteria employed during the weir survey (Table 2.1), is provided in Table 2.3.

Table 2.2 Gauging weir coordinates and information on historical flow records for the eight pilot sites (DWA 1990; DWAF 1991, 1994, 1997; P. Rademyer, Hydrology Division, DWAF, Pretoria, pers. comm.; F. Mouski, DWAF, Western Cape, pers. comm.).

PILOT SITE	GAUGING WEIR REFERENCE NUMBER (PLACE NAME)	LATITUDE	LONGITUDE	CATCHMENT AREA ABOVE WEIR (km^2)	MAIN RIVER SYSTEM	START DATE - END DATE HISTORICAL FLOW RECORD	WEIR ACCURACY RATING/ DESCRIPTION
Bakkerskloof Stream	G1H018 (Zachariashoek)	33º49'21"	19º02'50"	3.40	Berg	07/06/1964 - ongoing	no accuracy rating; small weir pool; v-notch weir
Du Toits River	H6H007 (Purgatory Uitspan)	33º56'19"	19º10'17"	46.02	Breede	01/10/1964 – 31/08/92	poor accuracy; rating = 1, expected error 30-50%; broad-crested weir; flood peak magnitudes often not measurable due to weir overtopping; accurate at low flows
Elands River	❖ H1H017 (old weir) (Hawequas Bos. Res.)	33º44'00"	19º06'54"	61.20	Breede	❖ 11/03/1969 – 30/04/1991	❖ moderate accuracy; rating = 2-3, expected error 10-30%; discharges < 17.0 $m^3 s^{-1}$ of acceptable accuracy; winter high flows fairly unreliable (precise stage of overtopping unknown); periods of record 10/02/76-05/10/76 and 06/79-11/84 of low reliability
	❖ H1H033 (new weir) 168 m upstream of H1H017	33º44'05"	19º06'54"	62.00	Breede	❖ 30/04/1991 – ongoing; data cross-correlated with H1H017 by DWAF	❖ high accuracy; cross-correlation with H1H017 for 14 month period of overlap in data recording (04/1991-06/1992) indicated an acceptable degree of flow correlation
Hex River	H2H006 (Glen Heatlie)	33º34'39"	19º30'12"	703.00	Breede	02/09/1980 - ongoing	no accuracy rating; upstream of H2H003, weir pool backs up into long pool/run section
Langrivier	G2H007 (Jonkershoek)	33º59'13"	18º58'13"	2.50	Berg	01/10/1942 - ongoing	no accuracy rating, but probably high as well-maintained; v-notch for low flows and sharp-crest for higher flows
Molenaars River	H1H018 (Hawequas Bos. Res.)	33º43'24"	19º10'13"	109.85	Breede	27/02/1969 - ongoing	moderate accuracy; rating = 3, expected error 10-20%; velocity of approach possibly 20% higher than original estimate, particularly affecting high flow accuracy; accurate at low flows
Riviersonderend River	H6H008 (Swarte Water Nuweberg Bos. Res.)	34º03'44"	19º04'23"	38.57	Breede	01/10/1964 – 30/06/1992	high accuracy; rating = 4, expected error 5-10%; broad-crested weir; weir exceedences occur frequently, in almost every winter month, albeit of short durations; accurate at low flows
Zachariashoek River	G1H014 (Zachariashoek)	33º49'39"	19º02'08"	2.80	Berg	07/06/1964 - ongoing	no accuracy rating; v-notch weir; small, shallow weir pool

Table 2.3 General descriptions of the eight sites and the two locations within each site.

SITE (tributary of river system)	RIVER ZONE	DEGREE OF ANTHROPOGENIC DISTURBANCE IN CATCHMENT AND AT SITE	GENERAL CHARACTER OF TWO LOCATIONS WITHIN RIVER REACH REPRESENTED BY SITE
Bakkerskloof Stream (Wemmershoek R.)	mountain stream	very low: primarily fynbos; pine plantation starts *c.* 50 m downstream of the second location, which has 20% alien *Pinus* spp.; less disturbed site than Zachariashoek	well developed indigenous riparian fynbos, occasional pine trees in downstream location; open to partially open canopy; upstream location very short, less suitable in this respect than Zachariashoek; downstream location with more open canopy, but similar channel width to Zachariashoek, downstream of road culvert pipe; sandstones/quartzites; boulder/bedrock substratum with some cobble; riffles, pools and few runs; narrow channel that rapidly becomes steep and bedrock-dominated upstream; some instream *Isolepis digitata* and marginal stands of *Prionium serratum*
Du Toits River (Riviersonderend R.)	upper foothill, transitional to mountain stream	low: primarily fynbos; large, natural wetland system in valley downstream of site; some water abstraction near source	well developed indigenous riparian fynbos; open canopy; small wetland seeps along banks; primarily cobble bed; sandstones/quartzites; long sloping riffles and short runs, some riffle and run patches interspersed, few marginal or instream pools; occasional stands of *P. serratum*; some algae
Elands River (Molenaars R.)	lower mountain stream, transitional to foothill	low to moderate: primarily fynbos; trout farm and some water abstraction upstream; hiking trail and use of river for recreation and trout fishing	well developed indigenous riparian vegetation; open canopy; cobble/boulder bed; sandstones/quartzites; patches of riffle and runs, some riffle bars, occasional pools; scattered *P. serratum* and *I. digitata*
Hex River (Breede R.)	middle to lower foothill	high: mostly alien and karroid vegetation, little fynbos; upstream agriculture; water abstraction and irrigation return flows, N1 road and railway line	riparian vegetation primarily alien; cobble bed dominant; sandstones/quartzites/shales; riffle and run biotopes; moderate amount of green algae
Langrivier (Eerste R.)	mountain stream	very low: fynbos; regularly sampled as long-term biological monitoring site	entirely indigenous riparian vegetation; largely closed canopy; boulder/cobble bed; sandstones/quartzites; step riffles, small cascades, pools and patches of run; high biotope heterogeneity
Molenaars River (Breede R.)	foothill	moderate: some fynbos, *Acacia mearnsii* dominant upstream of site; trout farms further upstream, N1 road and bridge construction activities	largely indigenous riparian vegetation; open canopy; cobble/boulder bed; sandstones/quartzites/igneous rocks; bar and slope riffles, runs, several pools largely upstream of weir; *P. serratum* abundant
Riviersonderend River (Breede R.)	mountain stream	very low: primarily fynbos, above pine plantation; scattered pines on mountain slopes	well developed indigenous riparian vegetation; open canopy; cobble/boulder bed with some bedrock; sandstones/quartzites; riffles, runs and several pools; abundant *I. digitata* and occasional *P. serratum;* some green algae
Zachariashoek Stream (Wemmershoek R.)	mountain stream	very low: primarily fynbos; 15-20 m upstream of start of pine plantation; moderately disturbed immediately downstream of weir	well developed indigenous riparian fynbos; partly closed canopy; bed of gravel, cobble, boulders and bedrock, some sand; sandstones/quartzites; narrow step riffles, runs; marginal stands of *P. serratum*; little *I. digitata*

2.3.2 Methods of data collection and analysis

Catchment and hydrological data were collated and benthic macroinvertebrate, physical habitat, and water chemistry data were then collected for each location and site during March 1994, peak dry season (sampling dates are given in Table 2.4). Pilot sampling and analysis methods are detailed here only where they differed from those employed in the main study (Chapter 3).

Catchment characteristics and hydrological regime

Catchment characteristics and site gradients were determined from 1:50 000 topographical maps, using standard methods described in Gordon *et al.* (1992), and compared. Stream order was derived using Strahler's method (with intermittent streams assigned first order status). Average instantaneous discharges and wetted channel widths at low flows were calculated from four cross-sections established at each site (Sections 3.2 and 3.4). The data were used as indicators of relative river size. Historical, average daily flow records for seven of the eight gauging weirs were downloaded from the central DWAF Hydrological Information System (HIS) database, while data for Langrivier weir were obtained from Jonkershoek Forestry Research Station (FORESTEK). Average monthly discharges for the eight sites were generated using the programs detailed in Section 3.2. Standardisations (or normalisations) of average monthly discharge as both a percentage of average annual discharge and by catchment area were performed to eliminate scale effects due to river sizes, allowing direct comparison among sites of annual hydrograph shape (Gordon *et al.* 1992).

Water chemistry

Twenty-two physical and chemical constituents were measured in each location of each site, on the same days that invertebrate samples were taken, generating 48 complete data sets (see below for specific variables). Field sampling and laboratory methods are given in Section 3.3. Principal Components Analysis (PCA) in PRIMER (Section 3.5) was used for multivariate analyses, with data for each location pair averaged for site-level analysis. The analyses were used to assess the validity of the null hypotheses that there are no significant differences in water chemistry among the eight sites (H_01), or between each pair of locations at a site (H_02). Supporting classification and non-metric MDS ordination analyses, using normalised Euclidean distance, were also performed.

Instantaneous temperature was used in the PCA, because the temperature range shown by maximum and minimum temperatures reflected only the one-day diel change in temperature recorded during sampling. The percentage of dissolved oxygen (DO) was used in preference to [DO], as it reflected the relative difference between observed and saturation DO for a location. As [NO_2-N] and [NH_4-N] values were small relative to [NO_3-N] in most instances, these variables were combined as [Inorganic-N]. Draftsman plots were generated for all variables to check for non-normality in the raw data. The Kolmogorov-Smirnov (d) goodness of fit test for normality, recommended by Zar (1984) for continuous distributions, was applied to measured data

for each variable, using STATISTICA. All variables, except instantaneous temperature, pH and %DO exhibited significantly non-normal distributions and were $\log_{10}(x+1)$ transformed to remove right-skewness, as well as occasional curvilinearity. Based on significant intercorrelations exceeding *r* (correlation coefficient) = 0.95 (Section 3.4; Clarke and Ainsworth 1993), the data set was pruned to 11 variables. To reduce the similarly high positive collinearity between pairs of ions, cation and anion ratios were used (Section 3.3).

Physical habitat

A range of hydraulic habitat and other environmental data were recorded where each invertebrate sample was taken, producing 48 data sets (see below for specific variables). Water depth was recorded, and velocity measurements were made at 0.6-depth (from the water surface), 0.2-depth, 0.8-depth, and immediately above the river bed (near-bed velocity). Average velocity was then computed using the four-point method (Section 3.4). Point depths and average velocities were used to calculate corresponding Froude numbers as an integrated index of turbulence (Section 3.4; Gore 1978; Gordon *et al.* 1992). Fliesswasserstammtisch (FST)-hemispheres were used as a further index of near-bottom flow conditions, specifically as an integrator of point benthic shear stress (Statzner and Müller 1989; Statzner *et al.* 1991). The rationale, limitations and procedures of the method are detailed in Statzner and Müller (1989). Examples of the use of FST-hemispheres are provided in Statzner *et al*. (1990), Scarsbrook and Townsend (1993), and Lancaster and Hildrew (1993b). Densities corresponding to FST-hemisphere numbers 1-24 used in this study are listed in Statzner and Müller (1989, p. 448, Table 1). At each sampling point, the number of the heaviest FST-hemisphere moved along a horizontal plexiglass plane by prevailing flows was recorded in the field, and then converted to a minimum bottom shear stress (MBSS) on the basis of regression relationships between hemisphere density (x, g cm^{-3}) and shear stress (y, dyn cm^{-2}) established by Statzner *et al.* (1991, p. 230, Table 2). For the lighter FST-hemispheres 0-10, the following linear regression model was applied:

$$y = 7.32x - 6.60 \ (n = 35, R^2 = 0.983) \qquad \textbf{Equation 2.1}$$

For FST-hemispheres 13-24, a power regression model was applied:

$$y = x^{2.85} \ (n = 69, R^2 = 0.993) \qquad \textbf{Equation 2.2}$$

For hemispheres no. 11 and 12, the means of the predicted values from both linear and power models were used. A MBSS value of 0.771 dyn cm^{-2} was assigned for hemisphere 0 (a fictitious hemisphere of density 1.007 g cm^{-3}), which allows a numerical value to be given to flows which do not move the lightest hemisphere (Statzner *et al.* 1991).

Substratum composition was documented using some 25 variables, for each 0.1 m^2 surface area of riffle area from which invertebrates were sampled. The β-axis (diameter) of each substratum particle or group of particles within the 0.1 m^2 area was measured (Section 3.4), and sizes graded according to a standard Wentworth grade scale (Appendix 3.4). The overall d_{50} (median), maximum and minimum particle sizes (and hence category of bed material) for the substratum surface layer were calculated. Similarly, the d_{50}, range, percentage surface area and approximate number of stones were determined for the dominant (DOM) and subdominant (SUBDOM) surface substratum elements by size. The percentage surface area and d_{50} values for the remaining surface substratum bed elements ("OTHER") were also calculated. The number of layers of substratum down to bedrock and fines was approximated. For the underlying layer(s) ("Subsurface"), the d_{50}, maximum and minimum particle sizes were calculated.

The percent embeddedness of the surface substratum elements in finer material was visually estimated before stones were removed for measurement. Substratum compaction, defined as the relative degree to which stones proved difficult to dislodge from the surrounding bed material, was estimated according to a nominal scale from low (entirely loose, 1) to high (immovable, 5). Substratum particle shape was visually estimated as: (1) angular, (2) sub-angular, (3) sub-round, (4) round, or a range of categories. Surface heterogeneity of the river bed at each sampling point was measured using a modified version of the substratum microprofile measuring device devised by Gore (1978). The perspex sampler sheet of 21 rods was made to fit within the frame of the benthic box sampler, thereby representing total sample area. The microprofile index was calculated simply as the standard deviation (SD) of the mean rod height above the sampler plate; there was no case where a single stone occupied about half the sampling area, potentially generating a value that could be confounded with that of an evenly distributed bed. Coefficients of variation were calculated from the microprofile data (Section 3.2). Increasing substratum heterogeneity was indicated by increasing microprofile index and CV values. The percentages and types of overhead and instream cover were visually estimated at each sampling point.

Prior to PCA to explore the extent of differences in riffle physical habitat among the eight sites and between location pairs, Kolmogorov-Smirnov normality tests were applied to the raw data. Variables with non-normal data distributions were $\log_{10}(x+1)$ transformed. Reduction of the variable set for PCA using correlation analysis was limited, as the majority of variables were only weakly correlated with one another, or significantly correlated only at $r << 0.95$ ($P < 0.05$); in the latter case mostly for substratum descriptors. The strongest relationships were found between average and near-bottom velocity ($r = 0.97$), and Froude number (Fr) and average ($r = 0.93$), and near-bottom velocities ($r = 0.91$). Hence, only near-bottom velocity and measures of overall substratum particle size were excluded from PCA. In the latter instance, DOM and SUBDOM particle size distribution ranges were used preferentially, while MI CV was included over MI as an index of substratum heterogeneity, as it showed better fit relationships with most other habitat variables. The PCA results were supported by ANOSIM analyses (Section 3.5), undertaken to test whether there were:

(1) no significant differences in riffle physical habitat among the eight sites ($H_0$1); or (2) between locations at a site ($H_0$2).

Benthic macroinvertebrates

Six benthic macroinvertebrate samples were taken from cobble-boulder riffles at each site, three replicate samples from different riffles in each location (n = 48). The riffle biotope was selected as it typically exhibits the highest taxonomic diversity, and sometimes abundances, of all mineral biotopes (e.g. Logan and Brooker 1983; Orth and Maughan 1983; Pridmore and Roper 1985; Statzner *et al*. 1988; Brown and Brussock 1991; Palmer *et al.* 1991; Tharme and King 1994; Wohl *et al*. 1995), thus providing probably the most representative once-off indication of benthic composition. Invertebrates were sampled quantitatively using a standard short, 0.34 m x 0.34 m box sampler, with an 80 μm-mesh terminal collecting bottle. The sampler covered 0.1 m^2 of river bed surface, and brush sampling was standardised to a substratum depth of *c.* 0.20 m. Field preservation and laboratory techniques were identical to those of the main study (Section 3.5). Taxonomic identification was to the level of family or higher taxonomic unit (hereafter simply referred to as family). Numbers of individuals were counted and expressed as densities per 0.1 m^2 of riffle.

Exploratory analyses of assemblage composition were undertaken using the complementary multivariate methods of hierarchical, agglomerative classification and non-metric, multi-dimensional scaling (MDS) ordination in PRIMER Version 5.2.9 (Section 3.5). All taxa were included in the analyses, with mean family-level abundances fourth-root transformed prior to computation of Bray-Curtis similarities. Classification was based on group-average linking of samples. In order to achieve the first two objectives (Section 2.3.1), classification and ordination were performed at three levels of resolution.

1. Analysis of the mean numbers of individuals per family, where means were calculated from six replicate samples per site, to ascertain the overall degree of similarity between the eight sites.
2. Analysis of average family densities for three replicate samples from each of the two locations, to identify the degree of inter-reach similarity in faunal composition.
3. Independent analysis of the total sample complement (n = 48), to provide an indication of natural variability in assemblage composition of each river and the extent to which it influenced site groupings.

The main findings of these exploratory analyses were supported statistically by an analysis of similarities (ANOSIM) for a balanced design, using PRIMER (Section 3.5), for the following null hypotheses ($\alpha = 0.05$): $H_0$1: there are no significant differences among the eight sites in riffle invertebrate assemblage composition at the family taxonomic level; and $H_0$2: there are no significant differences in family-level invertebrate composition between locations within each of the eight sites. The SIMPER program (Section 3.5) was used to identify the taxa responsible for observed differences among *a priori* groups.

Univariate measures of assemblage structure, namely the total number of families/higher taxa (S), total number of individuals (N), Shannon-Wiener diversity index (H'), Margalef's richness index (d), and Pielou's

evenness index (*J'*) were generated for all sample data, using the DIVERSE program in PRIMER (Section 3.5). The indices were used to provide an indication of relative assemblage diversity at family level, as well as to test the following null hypotheses ($\alpha = 0.05$): $H_0 1$: there are no significant differences among the eight sites in riffle invertebrate assemblage diversity at the family level; and $H_0 2$: there are no significant differences in diversity at the two locations within each of the eight sites. Differences in diversity among sites were examined (STATISTICA Version 5.5), using non-parametric Kruskal-Wallis ANOVA by ranks followed by *post hoc* identification of sites responsible for the observed differences, using Mann-Whitney U tests as a non-parametric alternative to Tukey HSD tests (T. Dunne, Statistics Department, UCT, pers. comm.). To test for inter-location differences in diversity at each site, Mann-Whitney U tests were performed with *a priori* use of two-sided exact *P* values to designate degree of significance, so as to account for small sample sizes; the small potential error due to tied ranks is acknowledged (StatSoft 2001).

Relationships between the composition of riffle assemblages and both water chemistry and physical habitat conditions were sought, firstly using the BIOENV routine in PRIMER with weighted Spearman rank correlation and normalisation of the environmental data to Euclidean distance (Section 3.5). As a result of the large number (21) of physical habitat variables, only subsets of variables could be analysed in BIOENV. The more robust BVSTEP program, which utilises fixed starting proportions of variables (Section 3.5), was used for analysis of the entire data set. Following the BIOENV/BVSTEP procedures, simple linear, best subset, forward and backward stepwise multiple regression analyses of univariate measures of assemblage composition against all environmental variables were undertaken. Data were synthesised to the level of site locations ($n = 16$ sample means). The various analyses were used to develop a preliminary understanding of relationships between invertebrate assemblage structure and environmental conditions during the dry season, as well as to independently identify possible key chemical and physical habitat variables for the low flow experiment (as per objectives - Section 2.3.1).

2.3.3 Results

Comparison of catchment and site characteristics, and hydrological regimes

Summary catchment and river characteristics for the eight candidate experimental sites are provided in Table 2.4. All of the sites are located on the upper to middle (only the Hex R.) reaches of the rivers, at similar altitudes. They encompassed two groups on the basis of stream order, gradient, wetted width and discharge, with Bakkerskloof, Zachariashoek and Langrivier representing considerably smaller, higher gradient streams than the remaining sites (Table 2.4). The Molenaars and Hex rivers are the largest, with correspondingly high average wetted widths and instantaneous discharges (Table 2.4). Riparian vegetation typically comprises indigenous fynbos at all sites, although the Hex also includes karroid elements, and several sites had alien flora (Table 2.3). Morphologically, all sites represent single thread, alluvial channels, although Bakkerskloof and Zachariashoek have high proportions of bedrock. The sites have relatively heterogeneous substrata and high physical habitat diversity. Anthropogenic disturbance was low at and surrounding all sites except the Elands, Molenaars and Hex, which showed increasing levels of human influence (Table 2.3).

Comparison of annual hydrological regimes revealed a wide range in average monthly discharges between the lower (Bakkerskloof, Zachariashoek and Langrivier) and highest magnitude (Molenaars and Hex) sites (Figure 2.1a). However, all eight sites exhibit the same characteristic seasonal pattern of consistently low flows during the summer months and markedly elevated flows from early May to late August, when average monthly discharge was expressed as a percentage of average annual discharge (Figure 2.1b). Standardisation by catchment area showed a similar, but less distinct, pattern. During the summer months of December-March, average monthly flows in the three smallest streams are extremely low (Average Q_{max} = 0.053 m^3 s^{-1} for Langrivier; Average Q_{min} = 0.004 m^3 s^{-1}, for Bakkerskloof), while average monthly flows at the remaining sites do not fall below 0.225 m^3 s^{-1} (Du Toits). Instantaneous discharges may be even lower, for example, an instantaneous discharge of 0.001 m^3 s^{-1} was recorded for Langrivier during the field survey (Table 2.4). For all sites, lowest average monthly flow is experienced in February. Timing of peak winter flows is less consistent among sites, from June to August. Overall, highest discharges are attained in the Molenaars, especially during July (Q_{max} = 10.646 m^3 s^{-1}).

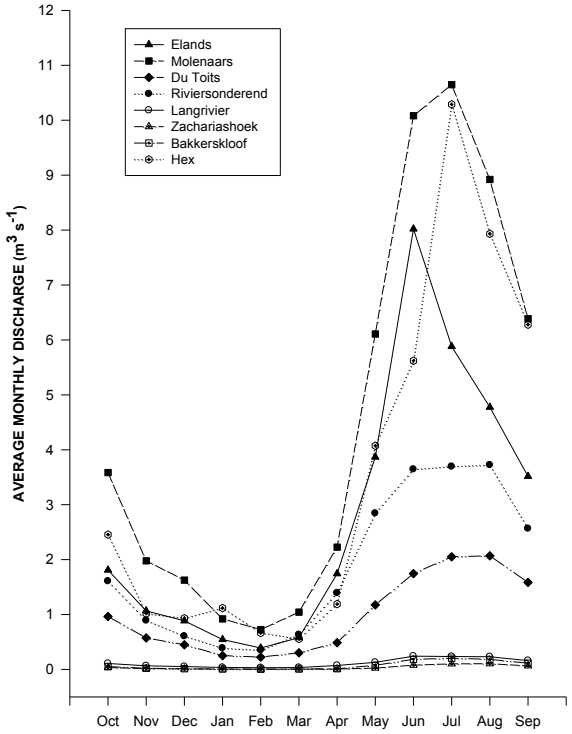
Table 2.4 **Select catchment and river characteristics for the eight pilot sites.** Site codes are indicated in parentheses. Site co-ordinates and catchment areas are provided in Table 2.2.

SITE	SAMPLING DATE	ALTITUDE (m a.m.s.l.)	*STREAM ORDER	DISTANCE FROM SOURCE (km)	GRADIENT (m/m)	WETTED CHANNEL WIDTH (m)	INSTANTANEOUS DISCHARGE (m^3 s^{-1})
Bakkerskloof (BA)	26/03/94	330	3	2.8	0.15	1.3	0.005
Du Toits (DU)	08/03/94	370	3	11.3	0.04	7.4	0.266
Elands (EL)	11/03/94	460	4	17.1	0.01	11.6	**0.682
Hex (HE)	15/03/94	310	5	38.0	0.006	15.8	0.635
Langrivier (LA)	22/03/94	390	3	2.9	0.10	2.8	0.001
Molenaars (MO)	10/03/94	370	5	12.7	0.01	17.2	**0.651
Riviersonderend (RI)	24/03/94	350	4	11.2	0.02	7.7	0.491
Zachariashoek (ZA)	17/03/94	310	3	2.5	0.15	1.3	0.006

* If stream order was calculated with the first perennial tributaries assigned first order status, all sites would be one stream order lower (Gordon *et al.* 1992).

** Although a higher instantaneous discharge was recorded for the Elands than the Molenaars River, this is atypical, with average daily discharges higher in the latter river (Figure 2.1a).

(a)



(b)

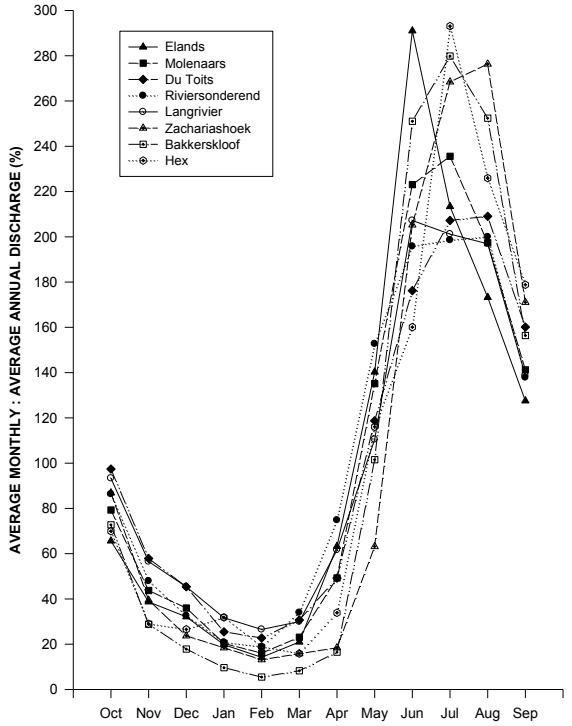


Figure 2.1 Characteristic annual hydrological regimes of the eight sites based on (a) average monthly discharges (m^3 s^{-1}), and (b) average monthly discharges as percentages of average annual discharge, to eliminate scale effects due to differences in river sizes.

Among and within site similarities in riffle faunal composition at natural low flows

Mean family-level abundances for the eight sites, and the two locations within each of them, are given in Appendix 2.2. Exploratory classification analysis of the overall degree of similarity among the eight sites indicated that the Hex site was markedly dissimilar to the other sites in riffle assemblage composition at only 51.4% similarity, while the latter group were at least 67.2% similar to one another (Figure 2.2a). The most similar sites were the Molenaars, Elands, Riviersonderend and Du Toits at 73.6% similarity, grouping separately from the Zachariashoek, Langrivier and Bakkerskloof sites (internally 70.4% similar). The Elands and Riviersonderend sites were most similar overall, at 80.7% (Figure 2.2a). The main site groupings were supported by the ordination results (Figure 2.2b), with no prospect of misinterpretation (Clarke and Warwick 2001).

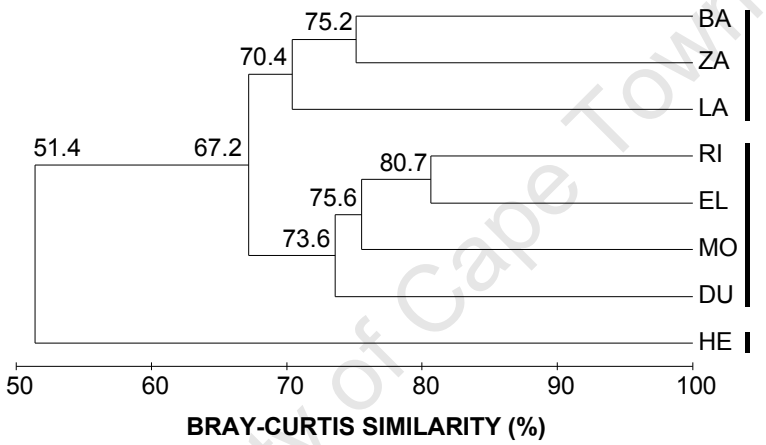


Figure 2.2 (a) Dendrogram showing hierarchical agglomerative classification with group-average linking, of the eight sites, based on average sample abundances (*n* = 6) for all families of benthic macroinvertebrates per 0.1 m^2 of riffle. Site codes are as per Table 2.4. Solid bars represent the three major groups and percentage similarities are given for each of the main dendrogram divisions.

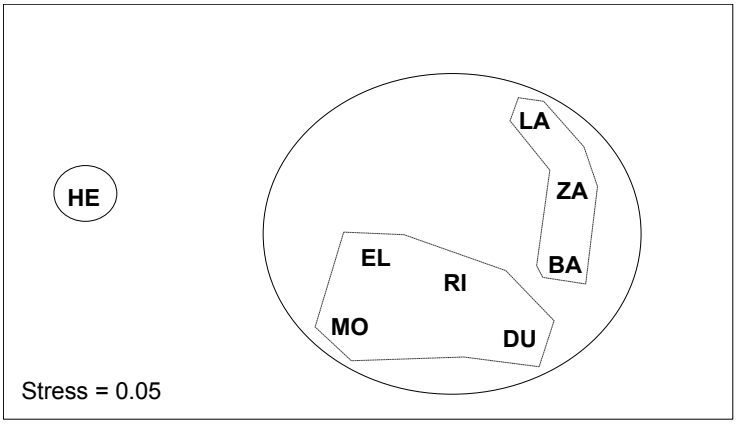


Figure 2.2 (b) Ordination using non-metric MDS, of the sites, based on the same similarity matrix as Figure 2.2a. Dendrogram clusters representing 60% (solid line) and 70% (dashed line) similarity have been superimposed.

As expected, within-reach differences in the composition of riffle invertebrate assemblages were lower than between-river differences, while the main site groupings represented in Figure 2.2 were retained (Figure 2.3). The two locations at the Molenaars site were the most homogeneous at above 89% similarity, but followed closely by the Elands, Du Toits and Riviersonderend sites, with all four rivers showing inter-reach similarities in riffle fauna greater than 86% (Figure 2.3a). For the Zachariashoek, Langrivier and Bakkerskloof sites, within-reach similarities in assemblage composition were slightly lower, but exceeded 76% (Figure 2.3a). Within-reach similarity was lowest overall for the Hex site, but still above 70% at family level. Classification results were well supported by the corresponding ordination, though relative inter-reach similarities were less differentiated (Figure 2.3b).

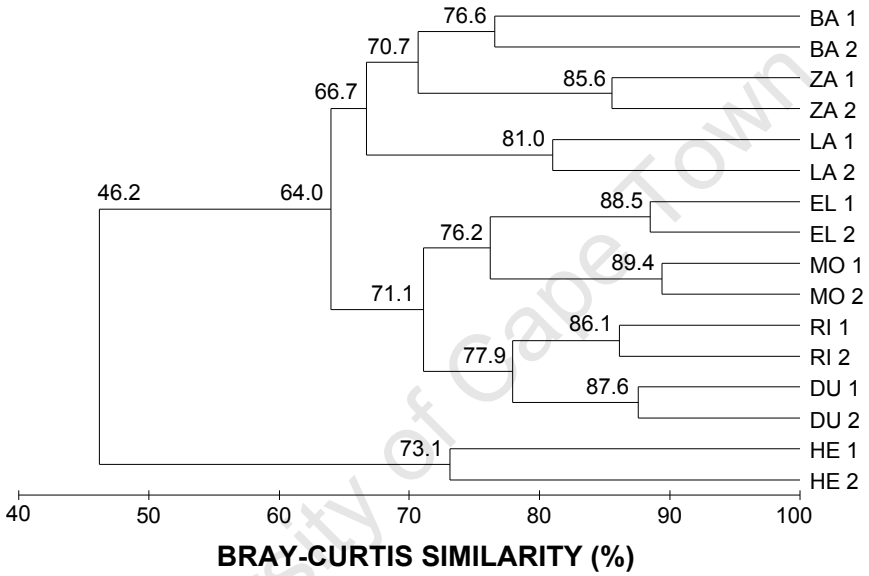


Figure 2.3 (a) Dendrogram showing hierarchical agglomerative classification with group-average linking, of the two locations at each of the eight sites, based on average sample abundances for each location (*n* = 3) for all families of benthic macroinvertebrates per 0.1 m^2 of riffle. (1) represents the upstream location and (2) the downstream location. Site codes are as per Table 2.4.

The relatively high natural variability in invertebrate assemblage composition within each site, on the basis of classification analysis using all 48 samples independently (Section 2.3.2), resulted in markedly lower percentage similarities among and within sites than at coarser levels of analysis and had some influence on the cohesiveness of site groupings (Figure 2.4a cf. Figures 2.2a and 2.3a). However, the clear division between the Hex and all other sites at very low percentage similarity was retained (Figure 2.4a). Moreover, the Du Toits, Molenaars, Elands and Riviersonderend sites still tended to cluster separately from the remaining sites. For all sites, intermixing of samples from separate locations (Figure 2.4a) supported the high degree of homogeneity in faunal composition previously observed (Figure 2.3a). Of the four sites exhibiting greatest internal cohesiveness in assemblage composition, namely Langrivier, Molenaars, Elands and Hex, lowest variability in assemblage composition was found for the Elands (89% similarity; Figure

2.4a). Clustering of the Elands and Molenaars samples reflected the tributary-mainstem relationship of the two sites. Unlike the Molenaars and Elands, which retained their independent faunal distinctness, the Riviersonderend site was extremely similar in benthic composition and within-reach variability to the Du Toits site (Figure 2.4a). This reflected, in part, the Du Toits River being a tributary of the Riviersonderend system (pre-Theewaterskloof Dam - Section 2.4). Of the Bakkerskloof, Zachariashoek and Langrivier sites, only samples from the latter site separated entirely as a group, with the other two sites showing high variability in benthic composition (Figure 2.4a). Ordination revealed a more gradual, uniform degree of separation between the group consisting of the Bakkerskloof, Zachariashoek and Langrivier samples, and the other sites (excluding the Hex) (Figure 2.4b), than reflected in the dendrogram. The low degree of separation of Riviersonderend and Du Toits samples confirmed strong biological similarities between these sites.

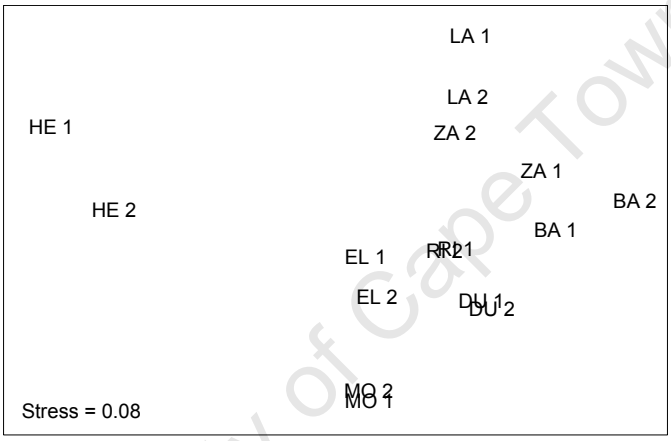


Figure 2.3 (b) Ordination using non-metric MDS, of the 16 locations, based on the same similarity matrix as Figure 2.3a.

The apparent high degrees of similarity in faunal composition within the reach representing each site (Figure 2.3) were supported by a two-way nested ANOSIM which showed that differences between locations (averaged across all sites) were not statistically significant (Global R = 0.009, $P = 0.434$), but that there were significant differences among sites. The null hypothesis ($H_0$2) that there are no significant differences in family-level invertebrate composition between locations within each of the eight sites was thus accepted. On the basis of these results, replicate samples from each location were pooled for a one-way ANOSIM test that indicated highly significant differences in invertebrate composition at the family level among the eight sites (Global R = 0.844, $P = 0.001$), allowing rejection of null hypothesis $H_0$1 (i.e. no significant differences among sites in riffle composition). Pairwise tests indicated that the differences among sites were significant over a range in R values of 1.0-0.591 ($P \leq 0.002$) for all sites except the Riviersonderend and Du Toits, which although significantly different ($P = 0.026$) represented the most similar pair of sites (R = 0.23). Maximum R values of 1.0 and hence, greatest differences were obtained between the Hex and all other sites.

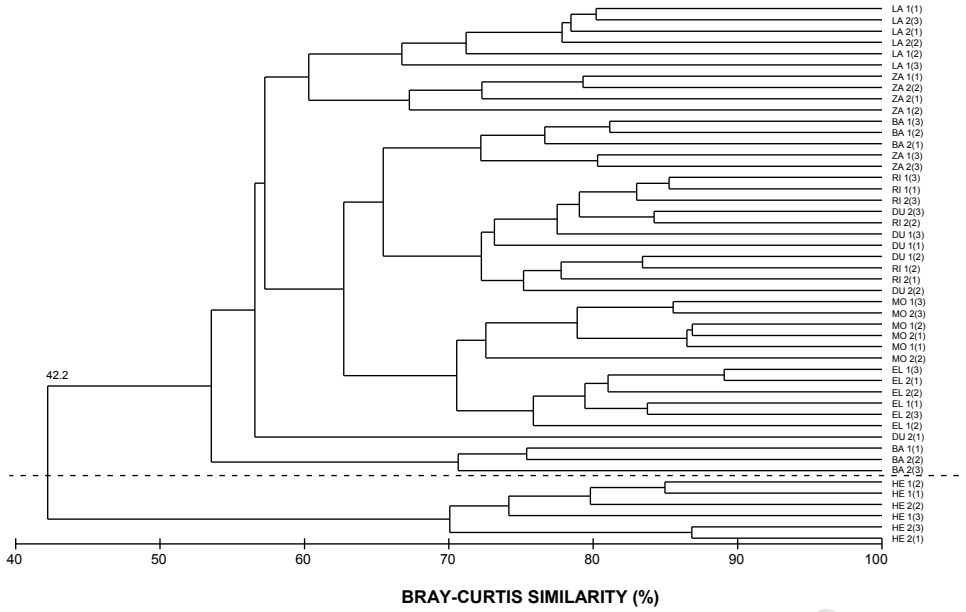


Figure 2.4 (a) Dendrogram showing hierarchical agglomerative classification, with group-average linking, of all 48 benthic macroinvertebrate samples collected from the eight sites. Samples represent family-level abundances, per 0.1 m^2 of riffle. Sample notation: 1(1) represents sample (1) from the upstream location, 2(1) sample (1) from the downstream location, etc. The main division into two groups, at 42.2% similarity (dashed line) is demarcated.

Figure 2.4 (b) Ordination using non-metric MDS, of all 48 invertebrate samples, based on the same similarity matrix and sample notation as Figure 2.4a. The discrete cluster of Hex samples is encircled, while the gradual separation of the other sites into two groups is indicated using a dashed line.

The results of a SIMPER analysis indicating which riffle taxa were primarily responsible for the differences between the various sites are detailed in Appendix 2.3. For the two site groupings for which invertebrate assemblage composition diverged most overall, namely the Hex site alone and a group comprising all other sites (Figures 2.2-2.4), the greatest difference (11%) could be attributed to markedly higher abundances of tricorythids at the Hex site ($\bar{x}$ = 248.0 ± 175.3 0.1 m^{-2}; Table 2.5), its third-most dominant riffle family (Appendix 2.2) and common in stony middle-reaches (King and Tharme 1994). Abundances of heptageniids were also far greater at the Hex site than at the other sites as were, to a lesser extent, those of Leptophlebiidae and Hydropsychidae (Table 2.5). Greater simuliid densities at all sites other than the Hex further contributed to group separation. Teloganodidae and Notonemouridae were entirely absent from the Hex, and there were low numbers of Elmidae, while these families comprised an integral component of riffle fauna at other sites (Table 2.5; Appendices 2.2 and 2.3). A large number of recognised upper-river southwestern Cape riffle families were also absent from the Hex reach: Teloganodidae, Notonemouridae, Philopotamidae, Athericidae, Hydraenidae, Leptoceridae, Helodidae and Limnichidae (Appendix 2.3).

Table 2.5 **Results of a SIMPER analysis comparing the average taxon abundances (0.1 m^{-2}) between the Hex site and a group representing the other seven sites (OTHER).** $\bar{\delta}_i$ = the contribution of the *i*th taxon to the overall average dissimilarity ($\bar{\delta}$) between sites, expressed as a cumulative percentage ($\Sigma \bar{\delta}_i$ %). Taxa are listed in order of decreasing contribution to dissimilarity, with an arbitrary cutoff at ≤ 50% dissimilarity. L = larva; P = pupa; L+P = combination, where larvae represent the majority in all instances. The higher abundance for each taxon between the two groups is highlighted in bold.

$\bar{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma \bar{\delta}_i$ %
OTHER and HEX = 57.79 %	OTHER	HEX				
Tricorythidae	0.26	**248.00**	6.12	4.63	10.59	10.59
Heptageniidae	2.81	**94.67**	4.19	2.12	7.26	17.84
Teloganodidae	**27.17**	0.00	3.13	2.42	5.42	23.26
Simuliidae (L+P)	**233.55**	18.67	3.01	1.24	5.20	28.46
Elmidae (L)	**39.31**	1.33	2.86	2.03	4.94	33.40
Hydropsychidae (L+P)	31.98	**100.67**	2.85	1.55	4.94	38.34
Leptophlebiidae	71.45	**123.33**	2.63	1.37	4.54	42.88
Notonemouridae	**14.50**	0.00	2.54	1.79	4.39	47.27

Comparison of the average family abundances between the group of small mountain streams, Zachariashoek, Bakkerskloof and Langrivier, and the group of four larger upper-reach sites, Du Toits, Elands, Molenaars and Riviersonderend (Figures 2.2-2.4), indicated that the primary difference in assemblage composition was in the abundances of the main 11 shared taxa, rather than as a result of the presence or absence of specific families (Table 2.6). In most instances, the four larger sites had higher invertebrate densities, particularly of the dominant riffle families, Chironomidae, Simuliidae and Baetidae, contributing a cumulative 17.8% to the overall average dissimilarity between site groups (Table 2.6). The shared character of the Zachariashoek,

Bakkerskloof and Langrivier sites was highlighted by the greater average abundances of Notonemouridae and Helodidae at these sites (Table 2.6 and Appendix 2.2), families typical of southwestern Cape mountain-stream zones and particularly sensitive to human impacts (Dallas *et al*. 1998, 1999).

Table 2.6 Results of a SIMPER analysis comparing the average taxon abundances (0.1 m^{-2}) between group (1) comprising the Elands, Molenaars, Riviersonderend and Du Toits sites, and group (2) comprising the Zachariashoek, Langrivier and Bakkerskloof sites.

$\bar{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma\bar{\delta}_i$ %
GROUP 1 and GROUP 2 = 43.39 %	GROUP 1	GROUP 2				
Simuliidae (L+P)	**393.96**	19.67	2.74	1.13	6.31	6.31
Chironomidae (L+P)	**593.67**	102.44	2.64	2.40	6.08	12.38
Baetidae	**285.13**	24.11	2.35	1.52	5.43	17.81
Athericidae	**8.25**	0.06	2.19	3.82	5.04	22.85
Hydropsychidae (L+P)	**52.38**	4.78	1.91	1.39	4.41	27.26
Leptophlebiidae	**110.38**	19.56	1.88	1.31	4.34	31.60
Acarina	**21.83**	3.06	1.77	1.48	4.08	35.68
Philopotamidae	**14.83**	1.39	1.55	1.38	3.58	39.26
Notonemouridae	3.71	**28.89**	1.53	1.49	3.52	42.78
Leptoceridae	**7.08**	1.22	1.43	1.26	3.29	46.07
Helodidae	3.67	**16.78**	1.39	1.33	3.21	49.28

Differences in assemblage composition among the four Group 1 sites, indicated in Appendices 2.3 and 2.4, can be attributed mostly to differences in the relative abundances of dominant families, most notably the far higher densities of simuliids ($\bar{x}$ = 1348.8 ± 1509.8 0.1 m^{-2}, compared with 16.2-179.3 individuals 0.1 m^{-2}), and to a lesser extent leptophlebiids, at the Molenaars site, compared with the other sites. Other key differences among sites included the absence of Philopotamidae and Heptageniidae at the Du Toits site, the absence of caenid mayflies at the Elands and Riviersonderend sites, and the similarly high numbers of Baetidae in the Elands and Molenaars rivers. Among Group 2 sites, differences in riffle assemblage composition were primarily due to differing relative abundances, although nematodes were absent from Langrivier and corydalid megalopterans from Zachariashoek, while Glossosomatidae only inhabited riffles in Langrivier (Appendices 2.3 and 2.4). Some of the main differences in riffle composition hinged on elevated numbers of hydraenids in Zachariashoek, and greater densities in Bakkerskloof riffles of Leptophlebiidae, elmid larvae, Helodidae and Teloganodidae. Moreover, higher numbers of simuliids occurred at Langrivier than in the other two reaches.

Inter- and intra-site similarities in riffle assemblage diversity at low flows

Means (± SD), maxima and minima for the five diversity measures calculated for each site are presented in Figure 2.5. The results of Kruskal-Wallis ANOVA by ranks and median tests to determine whether or not there were significant differences among sites in riffle diversity ($H_0$1) are presented in Table 2.7.

Table 2.7 Results of Kruskal-Wallis ANOVA by ranks and median tests for comparisons of diversity indices among the eight sites, including and excluding the Hex site. Site ranges for the various indices are presented in Figure 2.5, calculated at family level from riffle invertebrate abundances (0.1 m^{-2}). NS = not significant, * = significant ($0.01 < P \leq 0.05$), ** = significant ($0.001 < P \leq 0.01$), *** = highly significant ($P \leq 0.001$); exact probabilities rounded to three figures.

DIVERSITY INDEX	ALL SITES				EXCLUDING HEX			
	Kruskal-Wallis ANOVA (DF = 7, *n* = 48)		Median Test (DF = 7, *n* = 48)		Kruskal-Wallis ANOVA (DF = 6, *n* = 42)		Median Test (DF = 6, *n* = 42)	
	H	*P*	χ^2	*P*	*H*	*P*	χ^2	*P*
No. of Taxa (*S*)	20.175	0.005^{**}	9.934	0.192^{NS}	5.992	0.424^{NS}	9.034	0.172^{NS}
No. of Individuals (*N*)	36.129	0.000^{***}	26.667	0.000^{***}	32.199	0.000^{***}	26.667	0.000^{***}
Shannon-Wiener Diversity (*H'*)	27.306	0.000^{***}	21.333	0.003^{**}	23.462	0.001^{***}	24.000	0.001^{***}
Margalef's Richness (*d*)	24.753	0.001^{***}	17.333	0.015^{*}	12.144	0.059^{NS}	13.333	0.038^{*}
Pielou's Evenness (*J'*)	37.361	0.000^{***}	41.333	0.000^{***}	30.676	0.000^{***}	28.000	0.000^{***}

Significant inter-site differences were found for all diversity attributes, with the inclusion of the Hex site, allowing rejection of the null hypothesis, $H_0 1$ (Table 2.7). Median tests proved less useful in elucidating among-site differences indicating that although sample distributions may differ across sites, the medians of the distributions may not be notably different (likely a function of small sample sizes). Exclusion of the Hex from a subsequent ANOVA indicated this site was entirely responsible for observed significant differences among sites in both total numbers of families and taxon richness (Table 2.7). These results were supported by direct comparison of total numbers of taxa among sites, which revealed a wide overlapping range from a minimum of 12 (Bakkerskloof) to a maximum of 28 (Molenaars) for all sites excluding the Hex, for which the number of taxa ranged from seven to a maximum of only ten (Figure 2.5a). Similar trends were evident for family richness, with maximum recorded riffle richness for the Hex (1.256) lower than the minimum across the other sites (1.731) (Figure 2.5d). For total number of individuals, Shannon-Wiener diversity and Pielou's evenness, highly significant differences were found among sites, irrespective of the inclusion or exclusion of the Hex River (Table 2.7; Figures 2.5b, c and e, respectively). The results of pairwise *post hoc* comparisons among the sites for each of these diversity indices are provided in Table 2.8, indicating which sites were responsible for the observed differences.

Total numbers of individuals per 0.1 m^2 of riffle varied greatly among sites and samples, from as low as 100 (Langrivier) to a high of 5813, in the Molenaars (Figure 2.5b). Pairwise comparisons of site abundances showed that riffle invertebrate densities in the Molenaars River were significantly higher and more variable than those at any of the other sites, including the Hex ($U = 0.0$, $P = 0.002$; Table 2.8 and Figure 2.5b). The three smallest rivers exhibited significantly lower mean invertebrate abundances than all larger sites (100-1016 individuals 0.1 m^{-2}), but were not significantly different from one another in this regard (Table 2.8 and

Figure 2.5b). Total numbers of riffle invertebrates inhabiting the Du Toits, Riviersonderend, Elands and Hex sites were similar, from a minimum of 382 (Du Toits) to 2008 (Hex) individuals 0.1 m^{-2}. Riffle Shannon-Wiener diversity (*H'*) differed considerably among sites, with few consistent patterns (Figure 2.5c). The Molenaars did not differ significantly in *H'* from any other sites (Table 2.8), primarily due to high within-site variability in values ($\bar{x}$ = 1.646 ± 0.459). The Langrivier, Bakkerskloof and Zachariashoek sites all possessed similar, high riffle diversities, ranging from a minimum of 1.230 (Zachariashoek) to the overall maximum of 2.335 (Bakkerskloof). The Du Toits site exhibited the lowest diversity of all sites, including the Hex, and corresponding lowest assemblage evenness (Figures 2.5c, e) of the four sites grouped by multivariate analyses (Table 2.8). The Molenaars site showed high within-site variability in evenness (Figure 2.5e), as it did for the other diversity indices. The most anthropogenically impacted site, the Hex, had significantly higher assemblage evenness than all other sites (*U* = 0.0-2.0, *P* = 0.002-0.009), except Langrivier and Bakkerskloof (Table 2.8).

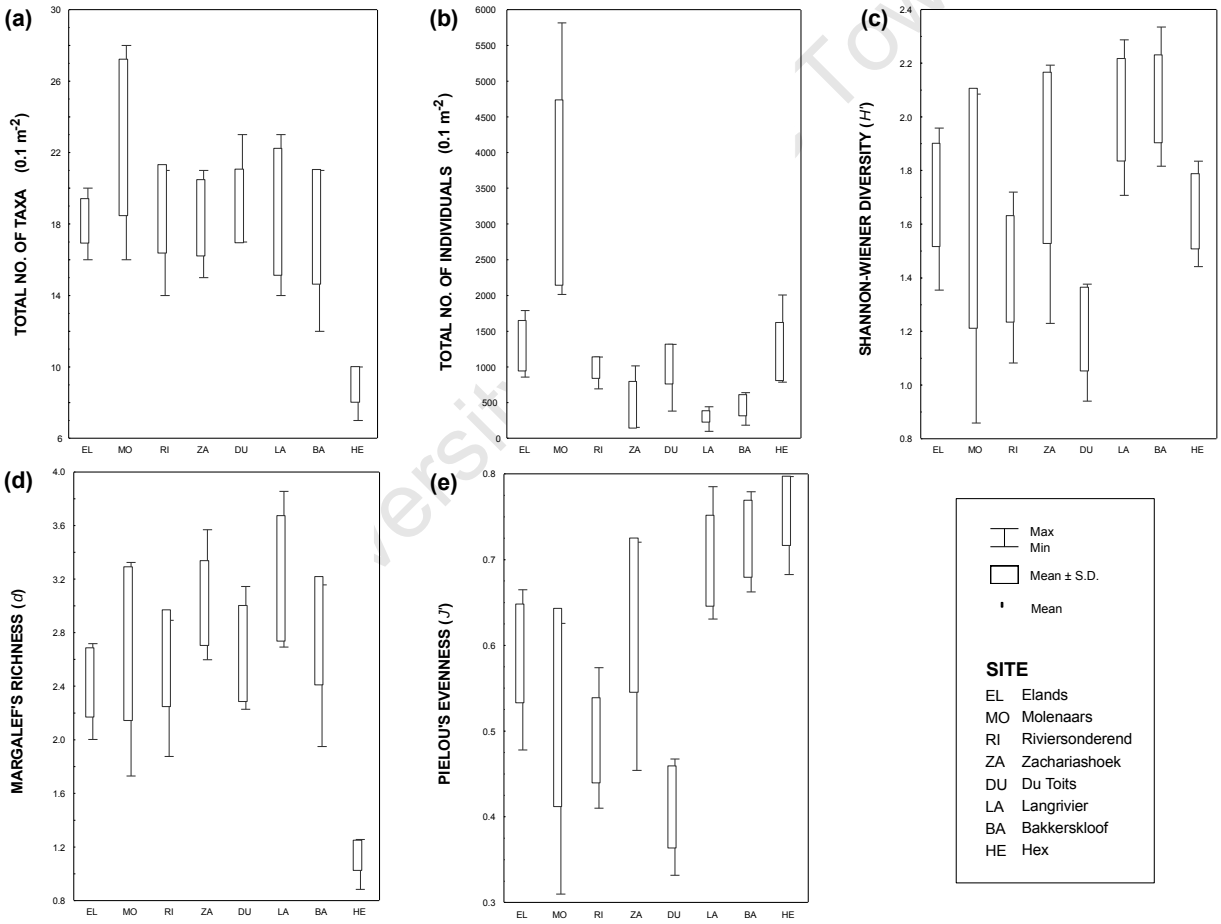


Figure 2.5 (a) Total number of taxa, (b) total number of individuals, (c) Shannon-Wiener diversity, (d) Margalef's richness and (e) Pielou's evenness, calculated for riffle assemblages at the eight sites.

Table 2.8 **Results of Mann-Whitney U tests of *post hoc* pairwise comparisons among the eight sites, for three diversity indices for which significant inter-site differences were apparent: number of individuals (*N*, 0.1 m^{-2}); Shannon-Wiener diversity (*H'*); and Pielou's Evenness (*J'*).** *P* values are presented, with the corresponding U statistic in parentheses (*n* = 6). No asterisk = not significant, * = significant ($P \leq 0.05$). Site abbreviations are expanded in Figure 2.5.

INDEX		SITE ARRAY							
		EL	**MO**	**RI**	**ZA**	**DU**	**LA**	**BA**	**HE**
	EL								
	MO	0.002* (0.0)							
	RI	0.180 (9.0)	0.002* (0.0)						
N	**ZA**	0.009* (2.0)	0.002* (0.0)	0.026* (4.0)					
	DU	0.589 (14.0)	0.002* (0.0)	0.485 (13.0)	0.015* (3.0)				
	LA	0.002* (0.0)	0.002* (0.0)	0.002* (0.0)	1.063 (18.0)	0.004* (1.0)			
	BA	0.002* (0.0)	0.002* (0.0)	0.002* (0.0)	0.589 (14.0)	0.015* (3.0)	0.240 (10.0)		
	HE	0.699 (15.0)	0.002* (0.0)	0.394 (12.0)	0.015* (3.0)	0.937 (17.0)	0.002* (0.0)	0.002* (0.0)	
	EL								
	MO	0.937 (17.0)							
	RI	0.093 (7.0)	0.310 (11.0)						
H'	**ZA**	0.240 (10.0)	0.589 (14.0)	0.041* (5.0)					
	DU	0.004* (1.0)	0.065 (6.0)	0.065 (6.0)	0.015* (3.0)				
	LA	0.015* (3.0)	0.132 (8.0)	0.004* (1.0)	0.485 (13.0)	0.002* (0.0)			
	BA	0.009* (2.0)	0.180 (9.0)	0.002* (0.0)	0.310 (11.0)	0.002* (0.0)	0.818 (16.0)		
	HE	0.485 (13.0)	0.699 (15.0)	0.093 (7.0)	0.132 (8.0)	0.002* (0.0)	0.009* (2.0)	0.004* (1.0)	
	EL								
	MO	0.394 (12.0)							
	RI	0.015* (3.0)	0.394 (12.0)						
J'	**ZA**	0.180 (9.0)	0.041* (5.0)	0.041* (5.0)					
	DU	0.002* (0.0)	0.093 (7.0)	0.015* (3.0)	0.009* (2.0)				
	LA	0.009* (2.0)	0.002* (0.0)	0.002* (0.0)	0.310 (11.0)	0.002* (0.0)			
	BA	0.004* (1.0)	0.002* (0.0)	0.002* (0.0)	0.041* (5.0)	0.002* (0.0)	0.699 (15.0)		
	HE	0.002* (0.0)	0.002* (0.0)	0.002* (0.0)	0.009* (2.0)	0.002* (0.0)	0.065 (6.0)	0.180 (9.0)	

Diversity indices for the two locations within each of the sites are given in Table 2.9. Results of Mann-Whitney U tests of whether or not each pair of locations differed significantly for each index ($H_0 2$) are summarised in the same table. No significant differences between locations at a site were found for any diversity indices or sites, with most locations exhibiting highly similar values for a particular index (Table 2.9). There were, however, several instances where test results indicated a tendency towards significance, at the 90% confidence level ($P = 0.1$), and where greater sample sizes might have shown significant differences. The sites where average between-location differences were most marked were Zachariashoek (diversity, richness and evenness), Bakkerskloof (diversity) and the Hex (total number of individuals) (Table 2.9). Total numbers of taxa represented the most consistent diversity measure between locations.

Similarities among and within sites in dry-season water chemistry

Chemistry conditions at the individual locations and site mean values are presented in Table 2.10. Variations in values between locations at a site were low. For most chemical variables, the Hex showed considerably higher summer values than the other sites (Table 2.10). This was especially the case for conductivity and TDS, where mean values for the Hex were 13.75 mS m^{-1} and 90.46 mg ℓ^{-1}, respectively, while averages recorded for the remaining sites ranged from 2.59 (Elands) to 4.58 mS m^{-1} (Zachariashoek), and 21.44 (Du Toits) to 31.06 mg ℓ^{-1} (Zachariashoek), respectively. Similar trends among sites were found for major ions and total alkalinity. The Hex and Molenaars were circumneutral, while all other rivers tended to have acidic waters. Particularly low pH values were recorded for the Riviersonderend and Bakkerskloof sites, at $\bar{x}$ = 4.5 and 4.6 units, respectively. Instantaneous water temperatures were relatively high, with high summer ambient air temperatures, ranging from 16.4 °C for the shaded, mountain-stream reach of Langrivier to 24.5 °C at the Hex site. Diel water temperatures peaked as high as 29.0 °C (Hex) and 27.0 °C (Du Toits) during the sampling period. Dissolved oxygen levels were high or near saturation at all sites, while TSS and turbidity values were uniformly low. Silicon concentrations were variable, but disproportionately higher for the Hex than other sites. The Elands exhibited the highest phosphate concentrations of all eight sites ($\bar{x}$ = 2.24 µmol ℓ^{-1}), and along with the Molenaars and Hex sites, had elevated dry season nitrate levels ([NO_3-N] = 15.885 - 36.755 µmol ℓ^{-1}). These sites were the most nutrient enriched and anthropogenically altered, although the former two sites still represented largely natural ecosystems (Table 2.3 and Section 2.4).

Ordination strongly supported the trends evident from summary statistics. As the PCA plots and eigenvector values were found to be highly similar at both site and location levels of resolution (as expected based on Table 2.10), only the latter results are presented (Figure 2.6 and Table 2.11). There were clear differences in water chemistry among the sites, where the first two principal components (PC1 and 2) generated in PCA explained a cumulative 71.2% of the variation, while addition of a third axis resulted in a total variance of 83.0% (PCA plot highly similar to that of Figure 2.6). There were no marked within-site differences in chemistry, although there was evidence of slight natural variation among locations (greatest for the Elands and lowest for Zachariashoek; Figure 2.6). At the resolution of individual locations, PC1 and PC2 explained 69.4% of the variation in water chemistry among site locations, while addition of a third axis resulted in a cumulative variance of 81.5% (Table 2.11); similar results were obtained at site level. Principal component scores for individual site locations are indicated by their relative positions along the main plot axes.

Table 2.9 **Results of Mann-Whitney U tests for comparisons of diversity indices between the two locations at each of the eight sites.** Adjusted 2*1-sided exact *P* values are presented to account for small sample sizes (*n* = 3 replicate samples per location). There are no significant cases ($P \leq 0.05$), but shading has been used to highlight cases with *P* = 0.1. Mean values (± SD) for the indices are presented, calculated at family taxonomic level from riffle benthic macroinvertebrate abundances (0.1 m^{-2}). LOC 1 = upstream location, LOC 2 = downstream location.

		DIVERSITY INDICES														
		No. of Taxa (*S*)			No. of Individuals (*N*)			Shannon-Wiener Diversity (*H'*)			Margalef's Richness (*d*)			Pielou's Evenness (*J'*)		
SITE	LOC	Mean (± SD)	*U*	*P*	Mean (± SD)	*U*	*P*	Mean (± SD)	*U*	*P*	Mean (± SD)	*U*	*P*	Mean (± SD)	*U*	*P*
EL	1	18.0 (1.0)	4.5	1.0	1154.3 (462.3)	2.0	0.4	1.671 (0.303)	4.0	1.0	2.437 (0.260)	4.0	1.0	0.577 (0.094)	4.0	1.0
	2	18.0 (2.0)			1348.3 (383.9)			1.722 (0.105)			2.376 (0.359)			0.596 (0.016)		
MO	1	24.0 (3.0)	3.0	0.7	3065.7 (681.8)	4.0	1.0	1.845 (0.176)	3.0	0.7	2.873 (0.402)	3.0	0.7	0.581 (0.033)	3.0	0.7
	2	21.3 (6.1)			3731.7 (1925.1)			1.448 (0.615)			2.517 (0.797)			0.467 (0.158)		
DU	1	18.0 (1.0)	3.0	0.7	1062.7 (80.1)	4.0	1.0	1.218 (0.241)	3.0	0.7	2.440 (0.136)	3.0	0.7	0.421 (0.077)	3.0	0.7
	2	19.7 (3.1)			929.7 (487.5)			1.175 (0.102)			2.800 (0.499)			0.395 (0.015)		
RI	1	18.0 (3.5)	3.0	0.7	1075.7 (59.5)	1.0	0.2	1.346 (0.229)	4.0	1.0	2.434 (0.483)	2.0	0.4	0.466 (0.048)	4.0	1.0
	2	19.3 (2.1)			816.3 (195.6)			1.497 (0.203)			2.739 (0.254)			0.505 (0.059)		
ZA	1	19.3 (1.5)	2.0	0.4	382.7 (336.3)	4.0	1.0	2.047 (0.137)	0.0	0.1	3.240 (0.292)	0.0	0.1	0.691 (0.028)	0.0	0.1
	2	17.0 (2.6)			468.3 (474.9)			1.624 (0.347)			2.754 (0.162)			0.572 (0.102)		
BA	1	19.3 (2.1)	1.5	0.2	472.7 (171.3)	4.0	1.0	2.170 (0.160)	0.0	0.1	2.998 (0.154)	2.0	0.4	0.735 (0.063)	3.0	0.7
	2	16.0 (4.0)			369.0 (239.5)			1.941 (0.109)			2.587 (0.552)			0.707 (0.037)		
LA	1	16.3 (3.2)	1.0	0.2	191.7 (97.4)	1.0	0.2	1.928 (0.194)	2.0	0.4	2.953 (0.344)	2.0	0.4	0.695 (0.081)	4.0	1.0
	2	20.7 (3.2)			334.3 (106.2)			2.103 (0.205)			3.409 (0.573)			0.695 (0.040)		
HE	1	8.0 (1.0)	0.5	0.1	854.7 (57.9)	0.0	0.1	1.570 (0.113)	2.0	0.4	1.038 (0.158)	2.0	0.4	0.757 (0.034)	4.0	1.0
	2	9.7 (0.6)			1489.3 (453.4)			1.702 (0.178)			1.191 (0.062)			0.750 (0.060)		

Table 2.10 Summary of water chemistry conditions at the eight sites and individual locations, during the dry season. LOC 1 = upstream location; LOC 2 = downstream location. *n.d. - not detectable; limit of detection for NH4-N = 0.1 mg ℓ-1 or 0.007 mol ℓ-1

	SITES AND LOCATIONS											
	DU TOITS			MOLENAARS			ELANDS			HEX		
VARIABLE	LOC 1	LOC 2	MEAN	LOC 1	LOC 2	MEAN	LOC 1	LOC 2	MEAN	LOC 1	LOC 2	MEAN
sampling date	08/03/94	08/03/94	08/03/94	10/03/94	10/03/94	10/03/94	11/03/94	11/03/94	11/03/94	15/03/94	15/03/94	15/03/94
minimum temperature (°C)	21.0	21.0	21.0	21.0	21.0	21.0	19.0	19.0	19.0	22.0	22.0	22.0
maximum temperature (°C)	27.0	27.0	27.0	21.0	21.0	21.0	24.0	24.0	24.0	29.0	29.0	29.0
instantaneous temperature (°C)	22.6	20.9	21.8	20.9	20.3	20.6	22.9	19.0	21.0	25.1	23.8	24.5
pH (pH units)	5.8	5.6	5.7	6.7	7.0	6.8	5.8	5.7	5.7	7.1	7.1	7.1
conductivity (mS m^{-1})	3.36	3.21	3.29	2.81	2.83	2.82	2.57	2.61	2.59	13.45	14.05	13.75
oxygen (mg ℓ^{-1})	8.2	9.2	8.7	8.4	8.7	8.6	7.8	7.9	7.9	8.2	7.8	8.0
oxygen (% saturation)	94.9	103.4	99.1	94.4	96.8	95.6	91.1	85.3	88.2	99.5	92.9	96.2
TSS (mg ℓ^{-1})	<< 0.001	<< 0.001	<< 0.001	0.001	0.001	0.001	<< 0.001	<< 0.001	<< 0.001	0.001	0.001	0.001
TDS (mg ℓ^{-1})	21.11	21.77	21.44	29.32	26.22	27.77	25.73	22.03	23.88	90.52	90.40	90.46
sodium Na^{+} (mmol ℓ^{-1})	0.198	0.203	0.201	0.169	0.175	0.172	0.150	0.168	0.159	0.547	0.547	0.547
potassium K^{+} (mmol ℓ^{-1})	0.008	0.005	0.006	0.018	0.021	0.019	0.010	0.012	0.011	0.054	0.054	0.054
magnesium Mg^{2+} (mmol ℓ^{-1})	0.046	0.049	0.048	0.036	0.036	0.036	0.037	0.037	0.037	0.301	0.305	0.303
calcium Ca^{2+} (mmol ℓ^{-1})	0.015	0.018	0.017	0.040	0.039	0.039	0.027	0.021	0.024	0.320	0.313	0.317
total alkalinity HCO_3^{-} (meq ℓ^{-1})	0.060	0.070	0.065	0.090	0.100	0.095	0.070	0.070	0.070	0.210	0.280	0.245
chloride $C\ell^{-}$ (mmol ℓ^{-1})	0.249	0.263	0.256	0.157	0.155	0.156	0.168	0.169	0.169	0.690	0.691	0.690
sulphate SO_4^{2-} (mmol ℓ^{-1})	0.019	0.018	0.019	0.016	0.016	0.016	0.014	0.014	0.014	0.464	0.477	0.471
phosphate PO_4-P (μmol ℓ^{-1})	0.105	0.080	0.093	0.900	0.945	0.923	2.210	2.270	2.240	0.275	0.200	0.238
nitrate NO_3-N (μmol ℓ^{-1})	0.435	0.500	0.468	15.450	16.320	15.885	24.285	22.720	23.503	36.585	36.925	36.755
nitrite NO_2-N (μmol ℓ^{-1})	0.085	0.040	0.063	0.200	0.220	0.210	0.180	0.200	0.190	0.820	0.860	0.840
ammonium NH_4-N (mmol ℓ^{-1})*	n.d.	0.000	n.d.	n.d.	n.d.	n.d.	0.000	0.000	0.000	0.000	0.000	0.000
silicon SiO_2-Si (μmol ℓ^{-1})	1.060	0.670	0.865	6.100	6.850	6.475	1.670	1.590	1.630	91.000	48.750	69.875
turbidity (visual assessment)	clear	clear	clear	clear	clear	clear	clear	clear	clear	clear	clear	clear

Table 2.10 Continued.

	SITES AND LOCATIONS											
	ZACHARIASHOEK			LANGRIVIER			RIVIERSONDEREND			BAKKERSKLOOF		
VARIABLE	LOC 1	LOC 2	MEAN	LOC 1	LOC 2	MEAN	LOC 1	LOC 2	MEAN	LOC 1	LOC 2	MEAN
sampling date	17/03/94	17/03/94	17/03/94	22/03/94	22/03/94	22/03/94	24/03/94	24/03/94	24/03/94	26/03/94	26/03/94	26/03/94
minimum temperature (°C)	19.0	19.0	19.0	16.7	16.7	16.7	19.0	19.0	19.0	19.0	19.0	19.0
maximum temperature (°C)	22.0	22.0	22.0	17.0	17.0	17.0	21.0	21.0	21.0	21.0	21.0	21.0
instantaneous temperature (°C)	21.3	19.5	20.4	16.4	16.3	16.4	20.6	19.1	19.9	19.8	18.7	19.3
pH (pH units)	5.0	5.0	5.0	6.0	6.2	6.1	4.5	4.6	4.5	4.5	4.7	4.6
conductivity (mS m^{-1})	4.68	4.48	4.58	2.96	2.92	2.94	2.87	3.07	2.97	3.47	3.17	3.32
oxygen (mg ℓ^{-1})	8.3	7.7	8.0	8.5	7.2	7.9	8.9	8.7	8.8	7.4	5.8	6.6
oxygen (% saturation)	94.2	83.4	88.8	87.2	73.8	80.5	98.4	93.4	95.9	81.6	62.0	71.8
TSS (mg ℓ^{-1})	<< 0.001	<< 0.001	<< 0.001	<< 0.001	<< 0.001	<< 0.001	0.001	<< 0.001	<< 0.001	0.001	0.001	0.001
TDS (mg ℓ^{-1})	27.86	34.26	31.06	24.33	24.63	24.48	20.28	24.33	22.31	23.64	26.67	25.16
sodium Na^{+} (mmol ℓ^{-1})	0.293	0.266	0.280	0.203	0.204	0.204	0.158	0.165	0.161	0.231	0.232	0.232
potassium K^{+} (mmol ℓ^{-1})	0.004	0.005	0.005	0.011	0.011	0.011	0.003	0.007	0.005	0.005	0.006	0.006
magnesium Mg^{2+} (mmol ℓ^{-1})	0.070	0.058	0.064	0.038	0.039	0.038	0.041	0.042	0.041	0.051	0.051	0.051
calcium Ca^{2+} (mmol ℓ^{-1})	0.014	0.010	0.012	0.021	0.021	0.021	0.010	0.009	0.009	0.014	0.015	0.014
total alkalinity HCO_3^{-} (meq ℓ^{-1})	0.060	0.060	0.060	0.110	0.100	0.105	0.070	0.060	0.065	0.050	0.060	0.055
chloride $C\ell^{-}$ (mmol ℓ^{-1})	0.393	0.400	0.396	0.199	0.194	0.196	0.207	0.196	0.201	0.298	0.297	0.297
sulphate SO_4^{2-} (mmol ℓ^{-1})	0.019	0.019	0.019	0.013	0.012	0.013	0.015	0.014	0.015	0.010	0.009	0.009
phosphate PO_4-P (μmol ℓ^{-1})	0.050	0.020	0.035	0.150	0.165	0.158	0.665	0.670	0.668	0.125	0.140	0.133
nitrate NO_3-N (μmol ℓ^{-1})	4.290	4.480	4.385	1.460	1.360	1.410	0.180	0.090	0.135	0.195	0.335	0.265
nitrite NO_2-N (μmol ℓ^{-1})	0.030	0.080	0.055	0.110	0.165	0.138	0.285	0.235	0.260	0.165	0.165	0.165
ammonium NH_4-N (mmol ℓ^{-1})*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
silicon SiO_2-Si (μmol ℓ^{-1})	0.720	2.080	1.400	5.365	5.420	5.393	0.420	0.630	0.525	1.560	2.080	1.820
turbidity (visual assessment)	clear	clear	clear	clear	clear	clear	clear	clear	clear	clear	clear	clear

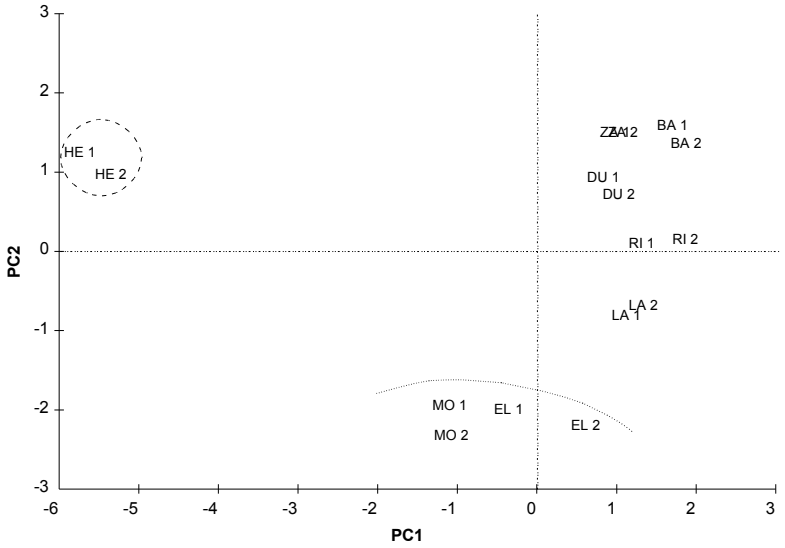


Figure 2.6 Loadings of individual locations on the first two principal components (PC1 and PC2), derived from PCA of water chemistry data for the eight sites. Site codes are expanded in Table 2.4. 1 = upstream and 2 = downstream location.

Table 2.11 Results of PCA of water chemistry data for the two locations at each of the eight sites. Eigenvalues, eigenvectors and percentages of variation are presented for the first three principal components, PC1-PC3 (see also Figure 2.6). * - indicates $\log_{10}$-transformed variables.

	PC1	PC2	PC3
Eigenvalue	5.5	2.1	1.3
Explained variance (%)	50.2	19.2	12.1
VARIABLE			
Instantaneous Temperature	-0.31	0.15	0.44
pH	-0.34	-0.27	-0.13
*Conductivity	-0.36	0.34	-0.03
Dissolved Oxygen	-0.17	-0.08	0.70
*Total Suspended Solids	-0.16	0.01	-0.35
Cation Ratio	0.42	-0.06	-0.02
Anion Ratio	0.12	0.58	0.19
*SO_4^{2-}	-0.39	0.21	-0.05
*PO_4-P	-0.03	-0.56	0.21
*Inorganic-Nitrogen	-0.34	-0.29	0.03
*SiO_2-Si	-0.39	0.02	-0.31

As envisaged on the basis of summary statistics (Table 2.10), cation ratio and $[SO_4^{2-}]$ were the primary contributors to the distinct separation between the Hex and the other sites (and respective locations) along PC1, although several other variables exhibited similar and relatively weak loadings (Table 2.11). Cation ratios were lower for the Hex locations, and hence concentrations higher (Equation 3.9) than for locations at the other sites, while $[SO_4^{2-}]$ values for the former were greatest overall ($\bar{x}$ = 0.471 mmol ℓ^{-1}). Similarly, for

PC2, a number of variables contributed to the explained variance, with the most influential being anion ratio and [PO_4-P]. Separation of the Elands and Molenaars from other sites was largely a result of higher principal component scores for the latter variable. The remaining group of locations within the Du Toits, Langrivier, Riviersonderend, Bakkerskloof and Zachariashoek sites shared low concentrations of cations and anions such as sulphates, but differed in natural nutrient levels. The PCA results were supported by identification of the same major site groupings through classification analysis and non-metric MDS ordination. All results strongly suggested that it was possible to reject hypothesis $H_0$1, that there are no significant chemical differences among sites, but not to reject $H_0$2, due to high intra-site similarities in chemistry.

Similarities among and within sites in riffle physical habitat at natural low flows

Summary statistics for physical habitat conditions in riffle biotopes at the eight sites are provided in Appendix 2.4. In terms of flow-related hydraulics, riffles at the naturally small, low discharge sites (Zachariashoek, Langrivier and Bakkerskloof) were shallower (average depth ($\bar{d}$) = 0.05-0.07, d_{min} = 0.03 m) than those at the remaining sites, which all had similar riffle depths at low flows ($\bar{d}$ = 0.10-0.15 m, with d_{max} = 0.20 m at the Du Toits and Elands sites). Average velocities ($\bar{v}$) and ranges were roughly the same for all sites, except Bakkerskloof, which tended to have slowest flow ($\bar{v}$ = 0.183 m s^{-1}); similar trends were apparent for near-bottom velocities. Highest mean riffle velocity was recorded for the Molenaars, while velocities reached a maximum (1.503 m s^{-1}) in the Elands. Average figures for the two composite hydraulic indices, namely Froude No. (Fr) and minimum bottom shear stress, MBSS, were lowest for the smaller streams, especially Bakkerskloof ($\bar{F}r$ = 0.283, mean MBSS = 1.76 dyn cm^{-2}). In contrast a far higher $\bar{F}r$ of 0.701 and mean MBSS of 45.69 dyn cm^{-2} were recorded in Molenaars riffles. Instream and overhead cover were low at most sites. The largely closed canopy of Langrivier was reflected in an average overhead cover value of 75%. Greatest instream cover occurred for riffles at the Bakkerskloof and Zachariashoek sites.

Riffle substratum was dominated by cobble at all sites, followed by boulders, with a wide overall range of substratum types encountered. The dominant substratum type by area was large cobble (129-256 mm), except at Zachariashoek, where small cobble predominated. The subdominant riffle bed material was large gravel at all sites except the Du Toits site, where small cobble was subdominant. Embeddedness of the substratum in finer material was generally low, as expected for the typically erosive biotope, reaching a maximum at Bakkerskloof ($\bar{x}$ = 14%) where lowest velocities occurred. All riffles exhibited a wide range in substratum heterogeneity and layering, with greatest complexity (CV = 0.7) and substratum depth (at least 2.0 layers) in the Molenaars River. The Bakkerskloof, Zachariashoek and Du Toits sites had the least complex subsurface substrata.

The high degree of variability in riffle physical habitat encountered among sites and the locations within them (Appendix 2.4) was a function of multiple factors. For the ordination analysis of the relative degree of similarity in habitat among the sites, PC1 and PC2 explained only 64.1% of the variation, while addition of

PC3 resulted in a total variance of 78.1% (Figure 2.7a). Major separation of the sites (along PC1) was driven by flow hydraulics, in particular MBSS and average velocity, as well as percentage embeddedness of riffle stones in fines (Table 2.12a). The latter substratum descriptor is itself strongly influenced by velocity. The widest separation among sites, between the Bakkerskloof and Molenaars rivers, mostly reflected the generally low and high values, respectively, for the suite of hydraulic variables (Appendix 2.4). Sites were further separated as a result of subtle differences in substratum composition and architecture (Table 2.12a).

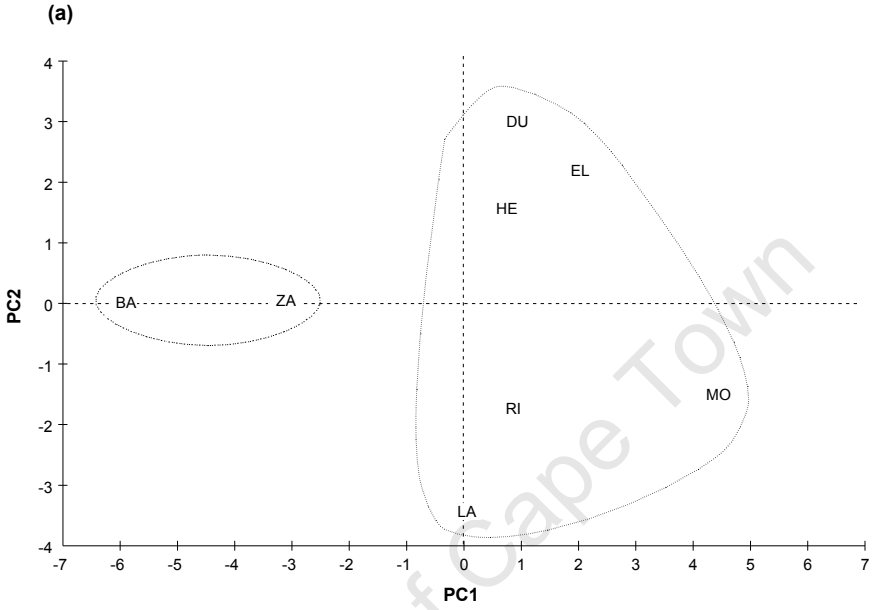


Figure 2.7 (a) Loadings of the eight sites on the first two principal components (PC1 and PC2), based on PCA of data on riffle physical habitat conditions. Site codes are expanded in Table 2.4. Major groupings, loosely based on a combination of PCA and ANOSIM results, are superimposed.

For PCA at the level of resolution of individual site locations, the first two components explained a lower percentage of the total explained variance in riffle habitat of 67% (Figure 2.7b and Table 2.12b). As at the site level, riffle hydraulic conditions, especially average velocity and related variables (e.g. MBSS), remained one of the key separators of (sites and) locations along PC1. Additionally, percentage substratum embeddedness and a number of substratum variables with similarly high coefficients, such as the maximum particle size of the dominant substratum (DOM SUBSTR max), number of substratum layers, and median size of subsurface sediments, contributed to the separation along the first axis (Table 2.12b). Much of the difference between location pairs at a site could be attributed to separation along PC2. Eigenvectors indicated that habitat variables primarily responsible for this separation were the maximum size of subdominant substratum elements, contrasted with the percentage area occupied by the dominant substratum material. The extent of divergence of location pairs varied considerably among sites, as a result of the high degree of variability in riffle complexity at different places within the same reach (Figure 2.7b and Appendix 2.4). Greatest separation between location pairs occurred at the Molenaars site, although it was not significant (ANOSIM results below). In contrast, habitat structure at the Bakkerskloof and Zachariashoek

locations was highly similar. The PCA results were somewhat supported by identification of the same major site groupings through non-metric MDS ordination, while the dendrogram from classification analysis accentuated the inherent natural intra-site variability in riffle architecture.

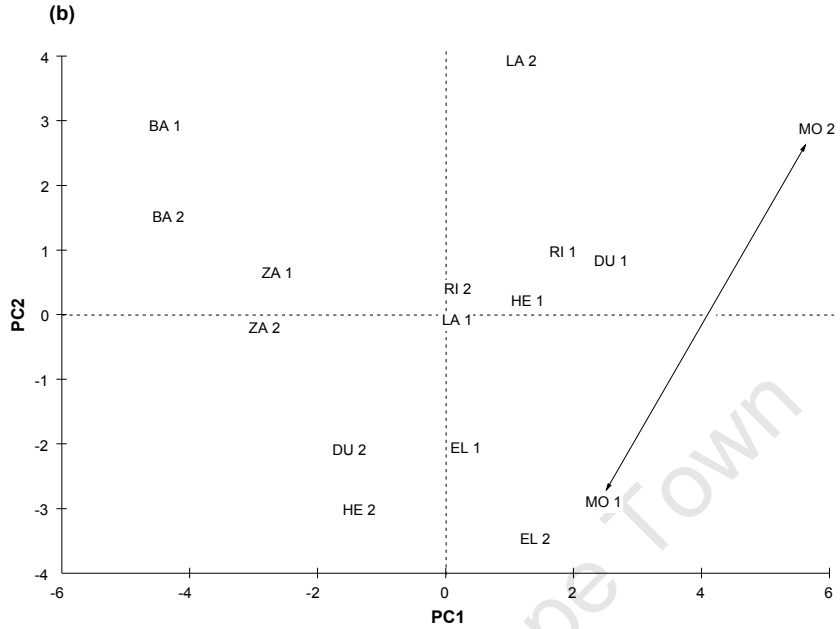


Figure 2.7 (b) Loadings of individual site locations on PC1 and PC2, derived from PCA of riffle physical habitat data for the sites. Site codes are expanded in Table 2.4. 1 = upstream and 2 = downstream location. Greatest dissimilarity between locations, indicated by the double-headed arrow, was recorded for the Molenaars site.

Ordination of the total sample data set (n = 48 samples) revealed high overall variability in riffle physical habitat, with very weak separation (and hence, considerable intermixing) of sites. Principal components 1 and 2 explained a low 41% of the variation, and PC3 only an additional 11%, with high levels of variability among individual samples obscuring clear patterns in habitat structure.

Two-way nested ANOSIM based on all variables describing riffle physical habitat showed that between-location differences (averaged across all sites) shown in the PCA results were not statistically significant (Global R = 0.12, P = 0.071), but that there were significant differences among sites. Pairwise tests showed that the most internally homogeneous pairs of locations in terms of riffle habitat were those of Bakkerskloof (R = -0.111, P = 0.90), Elands (R = -0.148, P = 0.90), and Zachariashoek (R = -0.111, P = 0.80). However, as suggested in the PCA plot, the Molenaars locations diverged most highly overall (R = 0.926, P = 0.10), indicating possible significant differences in riffle habitat between locations with greater sample sizes (Figure 2.7b). The null hypothesis ($H_0$2) that there are no significant differences in riffle habitat between site location pairs was accepted on the basis of these findings. Replicate samples from each location then were pooled for a one-way ANOSIM test of the degree to which the eight sites differed from one another.

Table 2.12 Results of PCA of physical habitat data for riffle biotopes (a) at the eight sites, and (b) within the two locations at each site. Eigenvalues, percentages of variation and eigenvectors are presented for PC1-PC3 (see also corresponding Figures 2.7a and b). * = log_{10}-transformed variables. Variable abbreviations: Median (d_{50}), minimum (min) and maximum (max) values are provided for dominant (DOM) and subdominant (SUBDOM) substratum (SUBSTR) particle sizes. OTHER - surface substratum remaining after DOM and SUBDOM components have been accounted for. Descriptors of subsurface substratum composition are also provided. Fr – Froude No.; MBBS - minimum bottom shear stress; CV - coefficient of variation.

	(a) SITE LEVEL			(b) LOCATION LEVEL		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	9.99	4.75	3.22	7.46	5.00	2.99
Explained variance (%)	43.4	20.6	14.0	32.5	21.7	13.0
VARIABLE						
Depth	0.252	0.238	0.105	0.172	-0.233	0.196
Average velocity	0.294	-0.042	0.075	0.313	-0.084	0.040
Fr	0.233	-0.219	-0.056	0.258	-0.016	-0.139
*MBSS	0.305	-0.023	0.016	0.278	-0.208	0.010
*Instream cover	-0.237	-0.002	0.221	-0.156	0.154	0.107
*Overhead cover	-0.059	-0.300	0.014	-0.025	0.182	-0.291
DOM SUBSTR area	0.142	0.261	-0.177	-0.008	-0.392	-0.045
DOM SUBSTR d_{50}	0.159	-0.145	0.351	0.218	0.246	0.143
DOM SUBSTR min	0.016	-0.077	0.444	0.133	0.301	0.182
*DOM SUBSTR max	0.221	-0.136	0.049	0.278	0.017	-0.034
*DOM SUBSTR no. of particles	0.203	0.240	-0.149	-0.010	-0.369	-0.056
SUBDOM SUBSTR d_{50}	0.043	0.119	0.453	0.128	0.142	0.464
SUBDOM SUBSTR min	0.097	0.287	0.328	0.134	-0.013	0.503
SUBDOM SUBSTR max	-0.055	-0.354	0.305	0.091	0.412	0.010
*SUBDOM SUBSTR no. of particles	-0.140	-0.332	-0.195	-0.084	0.216	-0.299
*OTHER d_{50}	-0.118	-0.350	0.008	-0.032	0.268	-0.161
*Subsurface area	0.270	-0.018	-0.254	0.262	-0.124	-0.226
Subsurface d_{50}	0.271	-0.153	0.003	0.305	0.095	-0.057
Subsurface min	0.270	0.026	0.168	0.271	0.082	0.121
Subsurface max	0.200	-0.328	-0.042	0.256	0.200	-0.264
*No. of SUBSTR layers	0.260	-0.181	-0.119	0.278	-0.038	-0.222
*SUBSTR embeddedness	-0.262	0.001	0.031	-0.272	0.014	0.036
Microprofile CV	0.255	-0.109	0.015	0.240	-0.129	-0.105

Highly significant inter-site differences in riffle physical habitat were found (Global R = 0.281, P = 0.001), allowing rejection of $H_0$1. Pairwise tests indicated that although the global R was low, differences between sites were significant for all combinations of sites except the following (in order of decreasing similarity): Hex and Elands (R = -0.074, P = 0.911); Hex and Riviersonderend (R = -0.019, P = 0.561); Molenaars and Hex (R = 0.059, P = 0.229); Hex and Du Toits (R = 0.069, P = 0.180); Elands and Du Toits (R = 0.083, P = 0.126); Molenaars and Riviersonderend (R = 0.122, P = 0.123); Molenaars and Elands (R = 0.156, P = 0.087); and Zachariashoek and Bakkerskloof (R = 0.124, P = 0.058). Hence, the two most similar sites with regards riffle habitat conditions were the Elands and Hex, as indicated by PCA (Figure 2.7a). In contrast, the greatest habitat differences were between the Molenaars, and Bakkerskloof (R = 0.719, P = 0.002) and Zachariashoek (R = 0.613, P = 0.002) sites, also supporting PCA results (Figure 2.7a). Correspondence

between site relationships derived from PCA and the ANOSIM results were weaker in most other instances. For the four sites that were found to group most closely in terms of riffle assemblage composition (Figure 2.2a), the Elands did not differ significantly from the others in riffle habitat. However, the Du Toits site differed significantly from both the Riviersonderend and Molenaars sites.

Relationships between riffle invertebrate assemblages and water chemistry at low flows

The results of BIOENV matching of the relative similarities found for riffle assemblages at site locations (Figure 2.3) with chemistry are summarised in Table 2.13. Individual chemical variables only weakly explained the separation of sites (and their location pairs - which were highly similar; Figure 2.6), with cation ratio providing the best single variable match ($\rho_w = 0.62$). Overall, the differences in invertebrate assemblage composition were best explained by a combination of nine variables, namely instantaneous temperature, pH, conductivity, DO, TSS, cation and anion ratios, $[SO_4^{2-}]$ and $[PO_4\text{-P}]$, at a high correlation of 0.75. Similarly high correlations, however, were obtained for far smaller groups of variables. In particular, a combination of cation ratio, anion ratio and $[SO_4^{2-}]$ yielded an acceptable match.

Table 2.13 Results of a BIOENV analysis of combinations of 11 chemical variables, taken *k* number of variables at a time, yielding the best matches as measured by weighted Spearman rank correlation (ρ_w) with the benthic macroinvertebrate similarity matrix derived for the locations at each of the sites. Bold italic type indicates the overall optimum combination of variables. Abbreviations for variables: instantaneous temperature (T); conductivity (C); dissolved oxygen (DO); total suspended solids (SS); cation ratio (CR); anion ratio (AR); SO_4^{2-} (S); PO_4-P (P); total inorganic nitrogen (N); SiO_2-Si (Si). Combinations of variables with tied correlations are indicated by "*or*".

k	BEST VARIABLE COMBINATION(S)	ρ_w
1	CR	0.62
2	AR, S	0.71
3	CR, AR, S	0.74
4	T, C, AR, S	0.72
5	T, C, CR, AR, S	0.74
6	T, pH, C *or* CR, DO, S, P	0.72
7	T, pH, DO, CR *or* C, AR, S, P	0.74
8	T, pH, DO, SS *or* C, CR *or* C, AR, S, P	0.74
9	***T, pH, C, DO, SS, CR, AR, S, P***	***0.75***
10	T, pH, C, DO, SS, CR, AR, S, P, Si	0.73
11	T, pH, C, DO, SS, CR, AR, S, P, N, Si	0.66

Results of simple linear regression of riffle diversity measures (Section 2.3.2) against chemical variables are presented in Table 2.14. There were no chemical variables that were consistently significantly related to all diversity measures, although DO showed significant relationships with four of them, excluding total number of taxa. The majority of highly significant relationships were obtained between total number of taxa, taxon

richness, evenness and dry season chemistry (Table 2.14). In this regard, individual cations and anions, ionic ratios and conductivity were influential chemical variables, supporting the PCA, ANOSIM and BIOENV results above. Highly significant negative relationships were found between number of taxa and concentrations of individual salts, as well as conductivity (R = -0.732, P = 0.000) (Table 2.14). The strongest relationship between number of taxa and ionic concentration was found for the cation [$Mg2^{+}$], while the highest significant relationship between anion concentrations and number of taxa was for [SO_4^{2-}]. While cation ratio was highly significantly positively correlated with the number of riffle taxa, anion ratio bore no significant relationship with the same diversity index. The number of taxa decreased significantly with increasing [SiO_2-Si], temperature and inorganic nitrogen concentration (Table 2.14).

Total number of individuals was weakly correlated with most chemical variables, but showed significant positive relationships with pH, DO, TSS, and the nutrients [Inorganic-N] and [PO_4-P] (Table 2.14). The only highly significant negative relationship was found between abundance and anion ratio (although not significantly related to individual salts; Table 2.14).

Shannon-Wiener diversity was poorly correlated with all variables, bar instantaneous temperature and DO where perhaps surprisingly in the latter case, weak but significantly negative relationships were obtained. The diversity-DO relationship represented the sole highly significant one. In contrast, more so than any other diversity attribute and with similar trends to those identified for number of taxa (to which it is akin), Margalef's richness was highly significantly related to most chemical variables (aside from total phosphorus concentration and anion ratio). The strongest regression relationship overall existed between cation ratio and family richness (R = 0.801, F = 82.092, P = 0.001; Table 2.14), reflecting consistently highly significant, negative relationships between this diversity measure and individual cations (e.g. Ca^{2+}). Similar, highly significant and negative relationships with individual anions were evident also, especially for [SO_4^{2-}]. Evenness of riffle assemblages at the sites was generally positively and significantly related to many of the chemical variables examined, especially individual salts (best-fit relationship obtained for Na^{+}; R = 0.541, P = 0.000), conductivity and TDS (Table 2.14), and [SiO_2-Si]. In addition, a highly significant negative relationship with DO was found. The proportion of total variability attributable to the dependence of evenness on each chemical variable tended to be low (indicated by very low R^2 values), however, and there were no significant relationships between taxon evenness and nutrient levels, TSS, anion ratio, temperature or pH (Table 2.14).

Attempts to identify broader groups of chemical variables largely responsible for differences in the above diversity attributes for sites (and locations) using multiple regression analyses, indicated that a high number of chemical variables was consistently required to generate best-subset relationships that explained a high proportion of total variability. Additionally, none of the regression R^2 values, after adjustment to account for the number of variables included, exceeded those obtained using single-variable regression.

Relationships between riffle invertebrate assemblages and physical habitat at low flows

No clear, well developed matches were found between riffle assemblage structure at the locations and physical habitat, based on multivariate BIOENV or BVSTEP results. Poor relationships ($\rho_w \leq 0.41$) were obtained for both single and multiple combinations of variables. Individual habitat variables only weakly explained the separation of locations on the basis of their riffle invertebrate assemblages. Although percentage instream cover provided the best single variable and overall match ($\rho_w = 0.41$), little reliance can be placed in the result, with the data set without doubt influenced by a preponderance of zero values. The next best single matches were with hydraulic (directly flow-related) variables, at far lower weighted Spearman correlations, namely MBSS ($\rho_w = 0.13$) and average velocity ($\rho_w = 0.12$). Similarly, poor matches were found for paired combinations of variables, with the highest correlations obtained for a combination of the hydraulic variables Fr and MBSS ($\rho_w = 0.20$), followed by average velocity and MBSS. All substratum variables appeared weak discriminators of inter-location assemblage composition, particularly individually. With the exclusion of instream cover, differences in invertebrate composition among locations were best explained (albeit still at a low level) by combinations of at least six to ten variables, all of which produced correlations in the order of 0.33. Of these, the group of fewest variables comprised Fr, MBSS, percentage overhead cover, substratum heterogeneity (CV), and the percentage of subsurface substratum area and its minimum particle size.

Linear regression analysis of measures of riffle assemblage diversity against the physical habitat variables of Table 2.15 indicated fewer significant interrelationships or distinct trends than for water chemistry. In stark contrast with the regression results for chemical variables, particularly, there were no significant relationships between the total number of riffle taxa at the eight sites (and locations) and any physical habitat variables. The strongest links between physical habitat and assemblage structure were for invertebrate abundance, although correlation coefficients were low in all cases. Total densities of individuals were highly significantly positively related to the maximum dominant particle size ($R = 0.509$, $F = 16.091$, $P = 0.000$) and hence, available surface area, and to MBSS (Table 2.15). A further ten weak yet significant relationships (mostly positive) were obtained between invertebrate densities and variables reflecting hydraulic conditions (e.g. velocities and depths), substratum complexity and character, as well as overhead cover (Table 2.15). Shannon-Wiener diversity bore clearer relationships with riffle habitat than with chemistry at the site locations (Tables 2.14 and 2.15). A highly significant, positive relationship was observed between diversity and overhead cover. In contrast with abundance, diversity decreased significantly with increasing substratum particle size (Table 2.15). Taxon richness was poorly related to physical and especially flow-related habitat conditions, being only weakly positively dependent on percentage overhead cover and number of subdominant stones (per 0.1 m^2), as well as decreasing with increasing stone roundness (and hence, surface area) (Table 2.15). Taxon evenness bore significant, negative relationships with velocity, depth and substratum size. Of all habitat variables considered, overall d_{50} particle size most influenced evenness, with increasing family dominance with increasing stone size ($R = -0.492$, $F = 14.673$, $P = 0.000$).

Table 2.14 **Results of simple linear regression analysis of five univariate measures of riffle benthic macroinvertebrate assemblage structure (family level) against 18 chemical variables, for a total of *n* = 48 invertebrate samples from the eight sites.** Chemical data are location-specific (*n* = 16 samples) and were not collected for individual invertebrate samples. Significant regression relationships are shaded. Variables are coded as follows: Temp. Inst. - instantaneous temperature; TDS - total dissolved solids; DO - dissolved oxygen; TSS - total suspended solids; Inorganic-N - total inorganic nitrogen. * - indicates $\log_{10}$-transformed variables.

CHEMICAL VARIABLE	NO. OF TAXA (*S*)			NO. OF INDIVIDUALS (*N*)			SHANNON-WIENER DIVERSITY (*H'*)			MARGALEF'S RICHNESS (*D*)			PIELOU'S EVENNESS (*J'*)		
	R	*F*	*P*	*R*	*F*	*P*	*R*	*F*	*P*	*R*	*F*	*P*	*R*	*F*	*P*
Temp. Inst. (ºC)	-0.435	10.730	0.002	0.232	2.619	0.112	-0.346	6.249	0.016	-0.660	35.515	0.000	-0.0007	0.033	0.857
pH (units)	-0.246	2.968	0.092	0.505	15.735	0.000	-0.073	0.243	0.624	-0.450	11.693	0.001	0.153	1.120	0.298
*Conductivity (mS m^{-1})	-0.732	53.042	0.000	-0.083	0.316	0.577	-0.013	0.007	0.933	-0.699	44.055	0.000	0.464	12.644	0.001
*TDS (mg ℓ^{-1})	-0.696	43.230	0.000	0.047	0.103	0.750	0.037	0.062	0.804	-0.717	48.634	0.000	0.502	15.514	0.000
DO (%)	-0.037	0.063	0.803	0.361	6.876	0.012	-0.541	19.069	0.000	-0.286	4.083	0.049	-0.447	11.488	0.001
*TSS (mg ℓ^{-1})	-0.144	0.978	0.328	0.388	8.128	0.007	0.080	0.298	0.587	-0.339	5.959	0.019	0.207	2.067	0.157
*Na^+ (mmol ℓ^{-1})	-0.731	52.819	0.000	-0.133	0.827	0.368	0.071	0.233	0.632	-0.653	34.285	0.000	0.541	19.013	0.000
*K^+ (mmol ℓ^{-1})	-0.630	30.222	0.000	0.246	2.958	0.092	-0.041	0.079	0.781	-0.757	61.902	0.000	0.403	8.905	0.005
*Mg^{2+} (mmol ℓ^{-1})	-0.749	58.871	0.000	-0.029	0.038	0.846	-0.036	0.060	0.807	-0.760	62.834	0.000	0.458	12.231	0.001
*Ca^{2+} (mmol ℓ^{-1})	-0.711	46.974	0.000	0.095	0.423	0.519	-0.051	0.120	0.730	-0.783	72.654	0.000	0.433	10.590	0.002
Cation ratio	0.648	33.384	0.000	-0.216	2.251	0.140	0.119	0.662	0.420	0.801	82.092	0.000	-0.338	5.922	0.019
*HCO_3^- (meq ℓ^{-1})	-0.641	32.079	0.000	0.141	0.935	0.339	-0.011	0.006	0.938	-0.696	43.313	0.000	0.424	10.059	0.003
*Cl^- (mmol ℓ^{-1})	-0.725	51.031	0.000	-0.225	2.456	0.124	0.029	0.038	0.847	-0.617	28.312	0.000	0.483	14.004	0.001
SO_4^{2-} (mmol ℓ^{-1})	-0.738	55.183	0.000	0.029	0.038	0.847	-0.065	0.196	0.660	-0.783	72.798	0.000	0.429	10.354	0.002
Anion ratio	-0.164	1.273	0.265	-0.543	19.240	0.001	0.015	0.011	0.918	0.054	0.135	0.715	0.066	0.200	0.656
PO_4-P (µmol ℓ^{-1})	0.190	1.714	0.197	0.431	10.502	0.002	-0.104	0.507	0.480	-0.107	0.530	0.470	-0.207	2.051	0.159
Inorganic-N (µmol ℓ^{-1})	-0.318	5.167	0.028	0.447	11.511	0.001	0.024	0.027	0.870	-0.537	18.653	0.001	0.262	3.402	0.072
SiO_2-Si (µmol ℓ^{-1})	-0.586	24.116	0.000	0.196	1.835	0.182	0.092	0.392	0.534	-0.645	32.775	0.000	0.505	15.733	0.000

Table 2.15 Results of simple linear regression of diversity measures for riffle invertebrate assemblages (family level) against a range of physical habitat variables, for a total of *n* = 48 invertebrate and corresponding abiotic samples from the eight sites. Significant regression relationships are shaded. Abbreviations: Av. - average; Bott. - bottom; MBSS - minimum bottom shear stress; OVER - overall particle size distribution; DOM - dominant particle size; SUBDOM - subdominant particle size; OTHER - remaining proportion of upper substratum layer; d_{50} - median; min - minimum; max - maximum; SUBSURF - subsurface substratum; no. - number of stones; CV - coefficient of variation. * - $\log_{10}$-transformed variables. [1]OVER max results were identical to those for DOM max.

PHYSICAL HABITAT VARIABLE	NO. OF TAXA (*S*)			NO. OF INDIVIDUALS (*N*)			SHANNON-WIENER DIVERSITY (*H'*)			MARGALEF'S RICHNESS (*D*)			PIELOU'S EVENNESS (*J'*)		
	R	*F*	*P*	*R*	*F*	*P*	*R*	*F*	*P*	*R*	*F*	*P*	*R*	*F*	*P*
Depth (m)	0.046	0.097	0.757	0.235	2.699	0.107	-0.363	6.966	0.011	-0.179	1.526	0.223	-0.338	5.923	0.019
Av. velocity (m s^{-1})	0.193	1.773	0.190	0.363	6.974	0.011	-0.242	2.869	0.097	-0.028	0.035	0.852	-0.335	5.816	0.020
Bott. velocity (m s^{-1})	0.186	1.646	0.206	0.360	6.836	0.012	-0.185	1.632	0.208	-0.023	0.024	0.878	-0.269	3.592	0.064
Froude No.	0.176	1.477	0.230	0.260	3.338	0.074	-0.109	0.548	0.463	0.030	0.040	0.842	-0.209	2.093	0.155
***MBSS (dyn cm^{-2})**	0.008	0.003	0.957	0.481	13.850	0.001	-0.230	2.566	0.116	-0.252	2.022	0.162	-0.205	2.022	0.162
***Instream cover (%)**	0.076	0.264	0.610	-0.073	0.246	0.622	0.264	3.449	0.070	0.092	0.396	0.532	0.199	1.898	0.175
***Overhead cover (%)**	0.123	0.707	0.405	-0.370	7.304	0.010	0.483	13.977	0.001	0.444	11.276	0.002	0.366	7.131	0.010
OVER d_{50} (mm)	-0.019	0.016	0.900	0.245	2.930	0.094	-0.504	15.640	0.000	-0.194	1.793	0.187	-0.492	14.673	0.000
OVER min (mm)	-0.054	0.136	0.714	0.292	4.302	0.044	-0.415	9.555	0.003	-0.250	3.057	0.087	-0.383	7.890	0.007
DOM d_{50} (mm)	-0.109	0.548	0.463	0.254	3.167	0.082	-0.240	2.811	0.100	-0.162	1.239	0.272	-0.199	1.902	0.175
DOM min (mm)	0.038	0.066	0.799	0.082	0.314	0.578	-0.018	0.014	0.905	0.045	0.095	0.759	-0.059	0.160	0.691
***[1]DOM max (mm)**	0.089	0.366	0.548	0.509	16.091	0.000	-0.006	0.002	0.968	-0.157	1.162	0.287	-0.033	0.050	0.823
***DOM no.**	-0.080	0.299	0.587	0.087	0.354	0.555	-0.222	2.376	0.130	-0.163	1.248	0.270	-0.155	1.132	0.293
SUBDOM d_{50} (mm)	0.067	0.208	0.651	0.255	3.200	0.080	-0.257	3.250	0.078	-0.059	0.161	0.691	-0.294	4.350	0.043
SUBDOM min (mm)	0.003	0.0005	0.983	0.325	5.449	0.024	-0.448	11.524	0.001	-0.182	1.583	0.215	-0.441	11.102	0.002
SUBDOM max (mm)	0.174	1.429	0.238	0.050	0.115	0.737	0.116	0.625	0.433	0.223	2.399	0.128	0.010	0.005	0.946
***SUBDOM no.**	0.278	3.839	0.056	-0.121	0.678	0.414	0.427	10.229	0.003	0.345	6.201	0.016	0.272	3.685	0.061
***OTHER d_{50} (mm)**	0.034	0.052	0.821	0.056	0.146	0.704	0.223	2.399	0.128	0.131	0.808	0.373	0.183	1.602	0.212
***SUBSURF area (%)**	0.047	0.100	0.753	0.433	10.637	0.002	-0.208	2.083	0.156	-0.228	2.531	0.119	-0.180	1.535	0.222
SUBSURF d_{50} (mm)	0.050	0.117	0.734	0.439	10.977	0.002	-0.378	7.658	0.008	-0.162	1.238	0.272	-0.358	6.743	0.013
***SUBSURF no.**	0.068	0.217	0.644	0.397	8.584	0.005	-0.142	0.949	0.335	-0.130	0.786	0.380	-0.142	0.950	0.335
Stone compaction	-0.186	1.652	0.205	-0.263	3.408	0.071	-0.123	0.707	0.405	-0.051	0.119	0.732	-0.032	0.048	0.828
Stone shape	-0.156	1.149	0.289	0.413	9.454	0.004	0.016	0.011	0.915	-0.385	7.999	0.007	0.146	0.997	0.323
***Embeddedness (%)**	-0.077	0.277	0.601	-0.198	1.872	0.178	0.371	7.343	0.009	0.040	0.072	0.789	0.391	8.299	0.006
Microprofile (mm)	0.020	0.018	0.893	0.233	2.633	0.112	-0.067	0.208	0.650	-0.046	0.096	0.758	-0.082	0.314	0.578
Microprofile CV	0.134	0.838	0.365	0.319	5.216	0.027	-0.091	0.384	0.538	-0.022	0.022	0.883	-0.165	1.284	0.263

Attempts to identify subgroups of physical habitat variables that might better link with riffle faunal diversity than single variables, based on multiple regression, gave the following results (Table 2.16).

Table 2.16 Regression summaries for forward stepwise multiple regression of five univariate measures of riffle assemblage diversity against physical habitat conditions. Physical habitat variables with significant partial regression coefficients (β_is) at $P \leq 0.05$ are highlighted in bold. Abbreviations are as per Table 2.15. * - $\log_{10}$-transformed. SE = standard error of estimate; DF = no. of degrees of freedom. ** = significant ($P \leq 0.01$), *** = highly significant ($P \leq 0.001$).

DEPENDENT VARIABLE	*n*	R^2 *(adjusted)*	DF	*F*	*P*	SE	SUBSET OF PHYSICAL HABITAT VARIABLES
No. of Taxa (*S*)	48	0.322	10, 37	3.230	**0.004	3.746	***SUBDOM no.**; **Av. velocity**; **DOM d_{50}**; **Microprofile CV**; Shape; OVER d_{50}; *DOM max; *MBSS; SUBDOM max; *DOM no.
No. of Individuals (*N*)	48	0.481	7, 40	7.215	***0.000	774.10	***DOM max**; ***MBSS**; **Compaction**; *SUBSURF area; SUBDOM min; Microprofile CV; *SUBDOM no.
Shannon-Wiener Diversity (*H'*)	48	0.497	8, 39	6.812	***0.000	0.256	**SUBSURF d_{50}**; **SUBDOM min**; **SUBDOM d_{50}**; ***SUBSURF area**; OVER d_{50}; Depth; *SUBDOM no.; *OTHER d_{50}
Margalef's Richness (*d*)	48	0.414	8, 39	5.143	***0.000	0.536	**Shape**; ***SUBDOM no.**; **Fr**; ***MBSS**; **Microprofile CV**; **DOM d_{50}**; **SUBDOM max**; *DOM no.
Pielou's Evenness (*J'*)	48	0.368	7, 40	4.916	***0.000	0.105	**Depth**; **Fr**; **SUBDOM min**; OVER d_{50}; *MBSS; Bott. velocity; Microprofile CV

As envisaged on the basis of the typically weak regression relationships obtained for single habitat measures (Table 2.16), subsets of at least seven variables were required to adequately explain variability in riffle assemblage diversity among locations. No habitat variables were linked consistently with assemblage structure across all diversity measures and, in several instances, the groups of significant variables were not the same as those independently found to explain most variability. Moreover, both hydraulic and substratum descriptors were included in all best regression subsets (Table 2.16), reflecting complex inter-variable relationships. Overall, about five habitat variables appeared to be most influential across all diversity attributes, namely substratum heterogeneity, number of subdominant particles, overall median and subdominant minimum particle sizes, as well as MBSS (Table 2.16). The best fit multiple-variable relationship was obtained for Shannon-Wiener diversity (R^2 = 0.497), where four substratum variables reflecting subdominant and subsurface substratum particle sizes and area were particularly significant. A similarly highly significant link was found between total number of individuals and a group of seven variables, notably maximum stone size, degree of substratum compaction and MBSS (R^2 = 0.481). The high number of variables (ten) in the subset and relatively low R^2 value obtained for total number of taxa (Table 2.16) confirmed the poor relationships obtained between this attribute and individual descriptors of physical habitat (Table 2.15).

2.3.4 Discussion and conclusions

The observed differences in catchment characteristics and subtle variations in hydrological regime for the eight rivers, and their probable varied influences on the biophysical characters of the sites, are acknowledged; the choice of potential study sites was limited from the outset (Section 2.2). Consequently, the pilot survey focused on addressing the extent of variability in invertebrate assemblage composition, physical habitat and water chemistry of riffles among and within sites, at spatial scales central to the proposed low flow study.

Among site variability in biophysical character

Apart from the Hex site, which differed markedly from the other sites in biophysical character, there was a relatively high degree of family-level similarity in riffle invertebrate composition among sites (67%). Clustering patterns of the seven remaining sites appeared to primarily reflect a separation, based on faunal differences, into (1) small, high gradient mountain streams located close to source (Zacharaishoek, Langrivier, Bakkerskloof), and (2) larger, somewhat lower gradient rivers located further down the river continuum, but still of mountain stream to foothill character. Tributary-mainstem relationships between sites or broad catchment affinities were reflected in the main site groupings (e.g. Molenaars and Elands, Riviersonderend and Du Toits). The natural cumulative effects of such influences of catchment (e.g. altitude, lithology) and derived properties (e.g. water chemistry, geomorphology) on aquatic invertebrate assemblages are well described (e.g. Vannote *et al.* 1980; Ormerod and Edwards 1987; Bournard *et al*. 1996; Clarke and Scruton 1997; Chessman 1999).

The individual character of the rivers was retained, however, with faunal differences between various site pairs significant in all instances. In the case of the Hex River, the singular presence of Tricorythidae and the absence of a large number of disturbance-sensitive or endemic southwestern Cape families (Dallas *et al*. 1999; Picker and Samways 1996) reflected its divergent characteristics relative to the other sites. These included its comparatively long distance from source, extent of human influence through land use (irrigated agriculture), and more arid climate (e.g. as reflected in the presence of karroid vegetation). For the other sites, inter-site differences were largely a function of relative differences in the riffle densities of different upper-river families (e.g. elevated hydraenid numbers at Zachariashoek). In some instances, particular families were entirely absent, for example, the absence of both Philopotamidae and Heptageniidae in the Du Toits reach. It is not possible to fully unravel the reasons for each river exhibiting a distinct riffle fauna, but regional biogeography and the effects of individual catchments acting as evolutionary units together played some part (Picker and Samways 1996; Wishart 2000; Wishart and Day 2002) alongside local influences, such as habitat and food availability (e.g. Wohl *et al.* 1995).

Despite observed significant differences in fauna even at the presence/absence level among all sites, the total numbers of families and (Margalef's) richness were stable measures of assemblage diversity across sites (with the exclusion of the Hex site), with no significant among-site differences. In contrast, total numbers of

individuals, Shannon-Wiener diversity and evenness differed more widely, proving better discriminators of individual sites.

Differences in chemistry among sites were clearly evident, with the greatest differences attributable to a combination of natural catchment influences and limited anthropogenic impacts. Of all chemical variables, the concentrations of cations and anions, as well as of nutrients (notably PO_4-P) most strongly discriminated among sites at low flows. Generally, however, regional chemical integrity was maintained (Day and King 1995) and chemical similarities among sites, other than the most impacted Hex River, were far greater than those recorded for riffle composition or physical habitat.

The character of riffle habitat was more variable among sites than invertebrate assemblage composition or chemistry, rendering it the least useful discriminator of site subgroups of high similarity. Both hydraulics and substratum composition varied significantly, and in complex ways, across sites. It was difficult to differentiate single or small groups of habitat variables with real discriminatory power from the wide array assessed. However, low flow conditions, particularly as represented by average velocity and hydraulic indices that integrate several aspects of flow, such as benthic shear stress, were principally responsible for inter-site differences in habitat quality; these results are supported by other studies (see Sections 1.2 and 8.1). Further differentiation among sites could be attributed to minor patterns of riffle substratum composition and architecture. Notably, the degree to which stones were embedded in fines, particle size ranges and relative proportions by area, for dominant, subdominant and subsurface components, as well as substratum subsurface complexity, showed some capacity for site discrimination.

Degree of within-site variability in biophysical character

Although there was evidence of some within-reach variability in the composition of riffle benthos (e.g. as shown in Godbout and Hynes 1982), intra-site faunal similarities exceeded 70% for all sites (attaining a maximum of 89%, for the Molenaars R.). Further, there were no significant within-site differences at either multivariate or univariate (individual diversity attributes) levels of assessment. Not all invertebrate diversity measures were equally consistent at a reach scale, though the total number of families was the most conservative feature of riffle assemblages. Within-reach chemistry also tended to be highly consistent, with relatively low levels of natural variability in evidence (e.g. Carlisle and Clements 1999). Within sites, riffle physical habitat was heterogeneous and more variable than chemistry, although observed differences in habitat between location pairs were not significant.

There was a lack of correspondence among the pairs of locations that showed the lowest variability in assemblage structure, chemical or physical habitat character. For instance, although the Molenaars reach exhibited the greatest similarity in riffle fauna between locations, it was also the most internally variable in terms of physical habitat. The result suggested that factors other than those examined might be at least in

part responsible for biotic variability (e.g. Power *et al.* 1988; Hildrew and Giller 1994; Wohl *et al.* 1995; Poff *et al.* 1997), including possibly biotic interactions (Peckarsky 1983; Peckarsky *et al.* 1997).

Riffle assemblage composition and water chemistry

While individual chemical variables tended to be weak discriminators of overall biotic differences among sites and locations with each reach, and suites of a high number of variables were needed to adequately describe relationships that explained a high proportion of total faunal variability in riffle assemblages across groups, ionic composition (and hence conductivity) was key (e.g. Dallas and Day 1993; Goetsch and Palmer 1997).

As expected, both positive and negative relationships were apparent between individual chemical parameters and attributes of benthic composition. Few relationships of consistently strong significance could be found between riffle invertebrate diversity and chemistry, though again conductivity and its constituent salts tended to be the most influential factors, particularly in terms of taxon richness. Although invertebrate abundances typically were weakly influenced by differences in chemical composition, increased nutrient concentrations were found to result in higher total numbers of individuals (Dallas and Day 1993).

The main chemical constituents responsible for site separation on the basis of chemistry alone, were also the central variables influencing invertebrate assemblage composition at single-attribute and multivariate scales. This suggested that water chemistry has a pivotal role in determining the invertebrate composition at a site along a river, particularly the complement of families represented; an outcome supported in the literature (e.g. Vannote *et al*. 1980; Wohl *et al*. 1995; Chapter 5).

Riffle assemblage composition and hydraulic habitat

Generally, relationships between characteristics of riffle habitat and benthic composition were poorly developed, though both flow-related hydraulic variables and substratum descriptors had an effect on assemblage structure. Riffle habitat appeared to have a more apparent, though typically weak, relationship with family abundances than with the numbers of families present, in contrast with the results obtained for chemistry. Indeed, significant relationships between numbers of riffle families and physical habitat were entirely lacking. Invertebrate abundances increased significantly, while Shannon-Wiener diversity and evenness decreased, with increasing size of dominant substratum elements (Newbury 1984). Total numbers of individuals also increased with increasing benthic shear stress, current speed, and other hydraulic factors.

The complexity of habitat-invertebrate interactions was exemplified by the high numbers of variables required in combination to adequately explain attributes of riffle biotic diversity. From a multivariate perspective, composite hydraulic indices, substratum availability and heterogeneity (Minshall 1984; Statzner *et al*. 1988) explained some of the biotic variability that was encountered, a result consistent with several other studies (Section 8.1). Although a vast number of studies have been conducted addressing relationships

between various attributes of benthic macroinvertebrate assemblages and hydraulic habitat characteristics (e.g. Barmuta 1989; Robson and Barmuta 1998; Wohl *et al*. 1995; Carter *et al*. 1996; Clarke and Scruton 1997; Jowett 2003), comparatively few of them have addressed a broad suite of substratum features. Pilot results highlighted the importance of considering not only the size distribution range for the dominant surface substratum, as commonly done, but also the composition of subdominant and subsurface materials. Furthermore, riffle architecture (Robson 1996; Robson and Barmuta 1998), notably substratum complexity and heterogeneity, were shown to be influential aspects of habitat; Downes *et al*. (1998a, b) showed the importance of such substratum features experimentally, and at fine levels of resolution. Relationships between physical habitat conditions at low flows, particularly in terms of hydraulic parameters, and links to invertebrate composition are discussed further in Chapters 6 to 8.

Site selection and potential constraints

From the standpoint of potential sites for a detailed low-flow investigation, the Hex site was unsuitable on biological and chemical grounds. This was despite its similarities with the other sites in seasonal flow pattern and riffle habitat. Although, from a physicochemical perspective, all of the remaining sites were sufficiently similar that they could be used for the low flow study, the most internally similar grouping of rivers in terms of assemblage composition was that of the Molenaars, Du Toits, Elands and Riviersonderend rivers - all tributaries of the Breede system. Within this group, the Elands and Molenaars rivers tended to form a subgroup, as did the other two rivers, reflecting catchment affinities. While the grouping of the smaller Langrivier, Bakkerskloof, and Zachariashoek rivers also exhibited high within-group biophysical similarities, pragmatic issues such as the area of wetted riverbed available for sampling (and thus the increased likelihood of over-sampling) and likely difficulties in measuring the naturally extremely low summer flows, precluded their selection. Additionally, a higher number of experimental sites was desirable. Hence, based on comparative results, the Du Toits, Elands, Molenaars and Riviersonderend rivers, each with two locations, were selected as sites for the low flow experiment described in Chapters 3-8 (see Section 2.4 for site descriptions).

A few potential constraints were identified to the interpretation of results from the planned comparative low-flow study, when dealing with sites of variously differing biophysical character. Observed differences between mountain stream and foothill reaches did not preclude the use of sites representing such zones, because biologically (at the family level) they were sufficiently similar. The pilot survey did, however, indicate the critical need for a control location at each site, as rivers retained some individual character despite often high degrees of biophysical similarity with other sites. As within-reach variability was shown to be largely insignificant, such control locations were expected to adequately reflect natural spatiotemporal trends in invertebrate composition, chemistry and physical habitat with low flow regime, for experimental purposes. In addition to providing a first understanding of relationships between abiotic conditions at natural low flows and assemblage composition, exploratory analyses suggested that univariate (including, but not restricted to diversity measures) and multivariate analyses of both physicochemical and hydraulic habitat

factors would be needed in any attempt to establish ecologically meaningful invertebrate responses to low flows. Further, they assisted in the identification of potentially suitable variables for use in the low flow study.

2.4 DESCRIPTIONS OF THE MAIN STUDY SITES

Descriptions of the present ecological character and extent of anthropogenic disturbance of the four main study sites (Figure 2.8 shows their locations), of relevance in understanding site-specific responses to low flow events, particularly for comparative purposes, are provided in this section. As a comprehensive assessment of the hydrological character of the rivers at the sites is central to this thesis and forms the subject of Chapter 4, only an overview of site hydrology is given here. Much of the biophysical information summarised below was derived from data collected during the pilot survey, and is supplemented by more extensive information in subsequent chapters.

2.4.1 Elands site

The location of the study site on the Elands River, some 60 km northeast of Cape Town (1: 50 000 topographical sheet 3319CA Bain's Kloof, 2nd ed. 1979, partially modified 1987) is indicated in Figure 2.8. Site co-ordinates and a brief description of the site are provided in Tables 2.2 and 2.3, respectively. Plate 3.1 illustrates the natural character of the site.

Catchment characteristics and hydrology

The catchment area of the Elands River upstream of the study site, some 17.1 km from the source, is the second largest of the four catchments at *c.* 61.0 km^2 (Table 2.2). The MAP for the Elands subcatchment, which represents a portion of WR90 quaternary catchment H10J, is estimated at 2207 mm (DWAF 1997). The MAE (S-Pan) figure is similar to that calculated by DWAF (1997) for the Molenaars site, at 1266 mm. The fourth order Elands River is perennial; information on runoff features and site hydrology is provided in Chapter 4. The river is the main tributary of the Molenaars River (Section 2.4.2), and hence part of the greater Breede system which enters the sea at Cape Infanta on the Cape southeast coast. The Elands feeds into the Molenaars near the eastern portal of the Huguenot Tunnel on the N1 freeway (Figure 2.8). It drains in a northerly direction, bounded on both sides by steep mountains. Flow contributions are received from numerous perennial and seasonal streams draining ranges including the Winterberg, Wemmershoekberge, Du Toitsberge and Tafelberg, with peaks at altitudes ranging from about 1995 m (Du Toits Peak) to 842 m. The main tributary, the Kraalstroom, has its source at about 1820 m.

The Elands catchment is largely undeveloped and without areas of commercial afforestation, irrigation agriculture or urban development (DWAF 1997). Anthropogenic disturbance is low at the site, although it is the second-most disturbed of the four sites overall (Table 2.3). Catchment vegetation comprises entirely

indigenous mountain fynbos in the vicinity of the site, on steep-sided valley slopes. Much of the catchment is managed by Cape Nature Conservation. A hiking trail runs alongside the river at the study site, and the area has further recreational value for flyfishing. A trout hatchery and associated farm are located on the Kraalstroom River, some 4 km upstream of the Elands study site. Although the hatchery has a detrimental impact on water quality and aquatic invertebrates for some distance downstream, the river has largely recovered once it reaches the study site (Ractliffe and Brown 1994). There was limited evidence of nutrient enrichment at the site at the time of this study (see below). Two DWAF hydrological gauging weirs are located on the Elands River at the lower extent of the study site, H1H017, which is no longer operational, and a new weir, H1H033 (Table 2.2; Figure 2.8). A bridge and retaining walls associated with the Huguenot Tunnel are located in the river reach just downstream of the site.

Geomorphology

The study site, at an approximate altitude of 460 m a.m.s.l. and with a moderately steep gradient of 0.01, represents the lower extent of the mountain stream zone and can be considered transitional to a foothill zone (Brown *et al.* 1996; Table 2.3). The river channel type is alluvial, largely single thread, of moderate width, and clearly defined. The reach is of the pool-rapid type (Rowntree and Wadeson 1999; King and Schael 2001). Medium to small boulders and large to small cobbles dominate the heterogeneous bed (Section 6.3.4, Figure 6.26). Sand and silt are uncommon, but there are localised gravel patches. Several bedrock outcrops occur instream and along the channel margins, a few due to valley inputs of scree. Biotope heterogeneity and hydraulic diversity are high, with dominant biotopes including pools, riffles, runs, transitional biotopes and backwaters (see Section 3.4.1, for definitions, and Chapter 6). The river banks comprise a mixture of sediments, but are dominated by bedrock, with sand and small boulders.

Riparian and instream vegetation

The riparian canopy is largely open at the site and comprises entirely indigenous mountain fynbos, of scrub and small trees (Table 2.3). No alien species are apparent. Instream vegetation is limited to occasional patches of *Isolepis digitata* and *Prionium serratum*. Although there is no background information on algal species composition or densities for the river, the presence of primarily green algae has been noted in summer and winter (Ractliffe and Brown 1994; pers. obs.).

Water chemistry

The pilot data were used to gain an understanding of natural background water chemistry for the site during the dry season (Table 2.10). Seasonal, long-term water chemistry data are available for weir H1H017, although nutrient data are rated of low reliability (Ractliffe and Brown 1994). A summary of historical trends is provided in DWAF (1991b, cited in Ractliffe and Brown 1994; see also Chapter 5). Historical ranges in chemical variables, especially for summer, corresponded well with the present-day data discussed below.

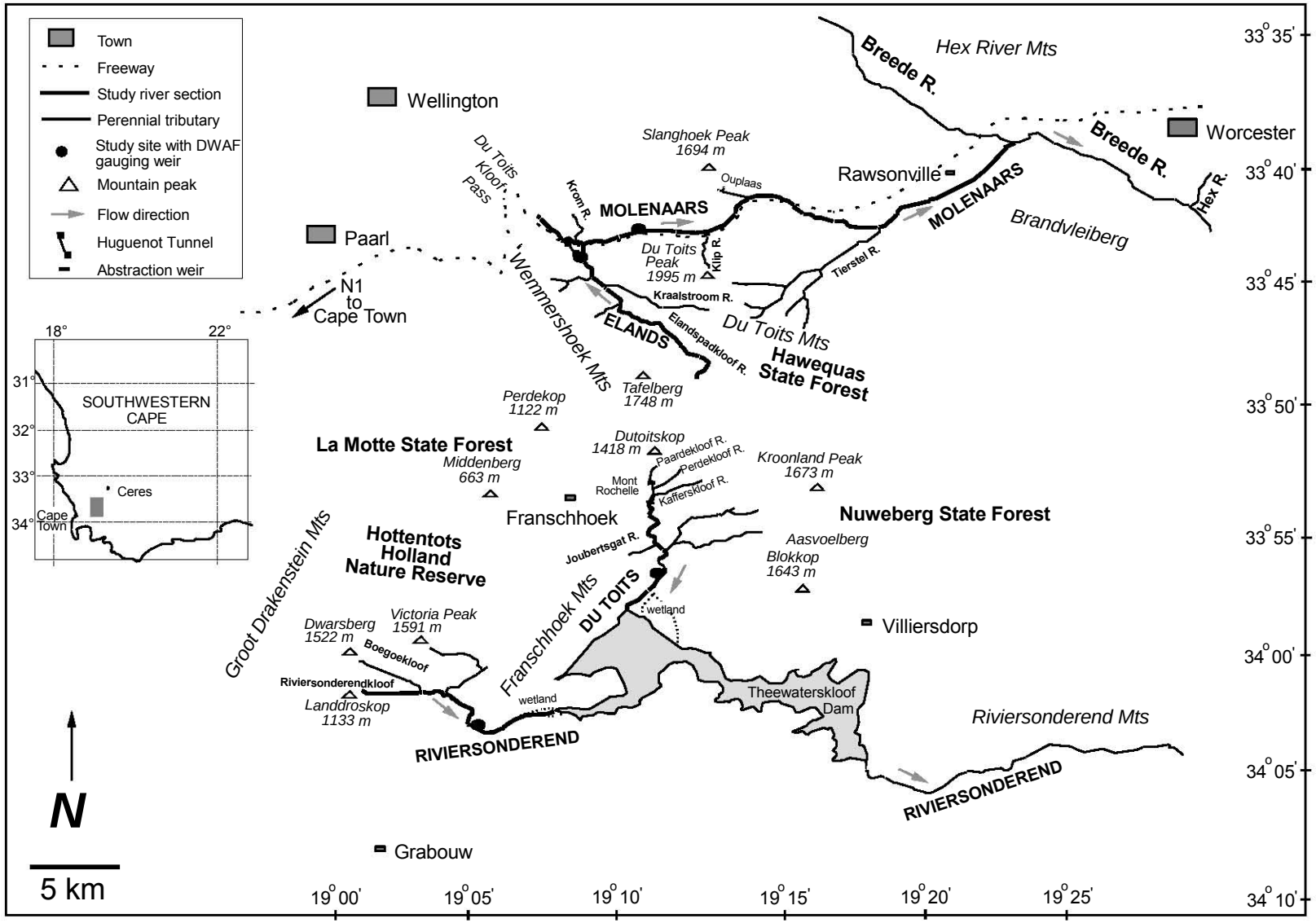


Figure 2.8 **Study area indicating the locations of the study sites on the Elands, Molenaars, Du Toits and Riviersonderend rivers, southwestern Cape (adapted from 1: 250 000 topographical sheets 3318 Cape Town 5th ed. and 3319 Worcester 3rd ed.).**

In March 1994, daily water temperature ranged from 19.0-24.0 °C, and was typically about 21 °C. The water was acidic, at an average pH of 5.7, which is just above the median background pH value of 5.5 for least-impacted southwestern Cape mountain streams (Dallas *et al.* 1998). Average total alkalinity (TA) was 0.070 mEq ℓ^{-1}. Conductivity was low (< 3 mS m^{-1}) and TDS values were correspondingly low (average of 23.88 mg ℓ^{-1}). Both these figures approximate regional median values for least-impacted mountain streams (Dallas *et al.* 1998). Ionic concentrations were all very low, with sodium and chloride characteristically dominant, at 0.159 mmol ℓ^{-1} and 0.169 mmol ℓ^{-1}, respectively. Oxygen levels were high, at 7.9 mg ℓ^{-1} (88.2% saturation). Levels of TSS were negligibly low, corresponding with the high water clarity at the site, and below regional median values for least-impacted, mountain stream zones (Dallas *et al.* 1998). Nitrate concentrations (an average of 23.503 μmol ℓ^{-1}) indicated mild nutrient enrichment. This enrichment and some impairment of water quality had been previously attributed to the establishment of the trout farm on an upstream tributary (Ractliffe and Brown 1994). Nitrites and phosphates were also elevated, at 0.190 μmol ℓ^{-1} and 2.240 μmol ℓ^{-1}, respectively. Ammonium levels were negligible. The summer concentration of silicon was 1.630 μmol ℓ^{-1}. There was little deposition of inorganic sediment at the site. The surfaces of the substratum were virtually free of algal growth, and only occasional patches of algae were evident during the dry season (pers. obs.).

Results from rapid bioassessment using the South African Scoring System (SASS - see below; Dallas *et al.* 1994) supported the findings of high water quality and very good general health of the river at this site.

Aquatic biota

The pilot study yielded a total of 28 benthic macroinvertebrate families/higher taxa for riffles, during the dry season, with relative abundances given in Appendix 2.2. The assemblage was insect-dominated, with nematodes, oligochaetes and planarians the only non-insect taxa. Sensitive invertebrates indicative of least impacted upper rivers included: Helodidae; Athericidae; Leptophlebiidae, Teloganodidae; Notonemouridae; cased trichopterans, including Barbarochthonidae and leptocerids; and Corydalidae. Tharme and Brown (1994) and Ractliffe and Brown (1994) recorded the following summer rapid bioassessment results, respectively: SASS scores of 232 and 199; total numbers of taxa of 30 and 23; and average scores per taxon (ASPTs) of 7.7 and 8.6. These results compare favourably with, and are within the upper limits for, SASS scores reported from relatively undisturbed rivers elsewhere in the southwestern Cape.

Fish recorded for the Molenaars system, and thus, potentially from the Elands tributary, are listed in Section 2.4.2. Two alien species are known to occur in the Elands, namely *Oncorhynchus mykiss* and *Micropterus dolomieu* (Ractliffe and Brown 1994).

Status of conservation and water resource development

The river reach encompassing the site has an abiotic conservation status of 83.4% (Class 2), that is, largely natural (Ractliffe and Brown 1994). The calculated biotic conservation status was lower, however, at 69.8% (Class 3). This represents a fairly high overall conservation status of 76.6% or Class 3, indicating that this section of the Elands is moderately modified. Although there has been a loss and change of natural habitat and biota, basic ecosystem functioning appears predominantly unchanged.

Presently, the Elands catchment is largely undeveloped in terms of its water resources, and there are no major or minor impoundments on the mainstream or any of the tributaries (DWAF 1994, 1997; Ninham Shand Consulting Engineers Inc., NSI, pers. comm.). Some water is diverted from weir H1H033 to cool the air conditioning system for the Huguenot Tunnel, and is reintroduced into the river further downstream. Presently, there is no other known abstraction of water in the vicinity of the site, although there is an un-quantified abstraction further upstream for the trout farm.

2.4.2 Molenaars site

The location of the study site on the Molenaars River (1:50 000 topographical sheet 3319CA Bain's Kloof, 2nd ed. 1979, partially modified 1987) is indicated in Figure 2.8. Site co-ordinates are provided in Table 2.2, and a brief description of the site is given in Table 2.3. Part of the catchment extends into the area described by 1:50 000 topographical sheet 3319CC Franschhoek (2nd ed. 1979, partially modified 1987). Plate 3.3 illustrates some of the site's natural features.

Catchment characteristics and hydrology

The catchment area of the Molenaars River upstream of the study site is the largest of the four at about 109.85 km^2 (Table 2.2), comprising a portion of WR90 quaternary catchment H10J (DWAF 1997). A description of the catchment of the lower Du Toit's Kloof Valley is given in HKS (1988). The river drains from west to east, forming a major tributary of the Breede system. The MAP of the catchment immediately upstream of the site is estimated as 1851 mm a^{-1} (DWAF 1997), with an overall MAP for this area combined with the Elands catchment (Section 2.4.1) of 2047 mm a^{-1}. The MAE has been calculated as 1266 mm a^{-1} (DWAF 1997). Site runoff characteristics, along with a description of the river's perennial flow regime, are documented in Chapter 4. A DWAF hydrological gauging station, H1H018, is located at the site, just upstream of the confluence of the Klip River, partway along the river valley (Table 2.2; Figure 2.8).

The Molenaars site is some 12.7 km from the source at the top of the Du Toit's Kloof Pass, in the Klein Drakenstein Mountains, at an altitude above 1000 m a.m.s.l. The river is also fed by perennial and seasonal streams and wetland seeps arising on the southern slopes of the Witteberg. Further drainage contributions to the river are from the northeastern slopes of the Klein Drakensteinberge, the northern DuToitsberge, and the southeastern slopes of the Slanghoekberge. The Molenaars flows eastwards, confined to the north and south

by mountain ranges from a maximum peak height of 1995 m (Du Toits Peak) to altitudes just above 800 m. The main tributary of the Molenaars is the Elands (Section 2.4.1), which joins it just east of the Huguenot Tunnel. The river leaves the Du Toit's Kloof Valley before its confluence with the Breede River at Worcester.

The catchment is vegetated primarily with indigenous fynbos, notably shrubland and woodland plant communities. Almost 25% of it is located within the Hawequas Mountain Catchment Area, where it is largely protected from anthropogenic disturbance, while the remaining area is government or privately owned land. Anthropogenic disturbance is moderate (Table 2.3), making this site the most disturbed of all four sites. There is no significant urban development in the catchment. The N1 national road, and associated Huguenot Tunnel and bridges, represent the dominant human influence in the area, as the road runs directly alongside the river. There is no irrigation, afforestation or water resource development in the upper catchment (as at 1993; DWAF 1997). However, an area of alien riparian vegetation of density greater than 25% occurred downstream of the confluence of the Elands River at the time of this study (DWAF 1997). During the study, large scale road and bridge construction, the latter crossing the river, was underway to widen the N1, both upstream and downstream of the study site (pers. obs.; Ractliffe and Brown 1994). In addition, an alien vegetation clearance programme by CNC had commenced upstream of the study site (pers. obs.; Ractliffe and Brown 1994). Two trout hatcheries are located on the mainstream, one of which is located on the mountain-stream zone upstream of the study site (the other farm is on the Elands, Section 2.4.1). Buildings and fruit orchards are located along the river reaches upstream of the study site, and protea farming also takes place in the Du Toit's Kloof Valley.

Geomorphology

A longitudinal profile of the river from its source to the end of the Du Toit's Kloof Valley is given in Ractliffe and Brown (1994). The river exhibits a steep gradient from its source for some 5 km, before the Krom and Elands tributaries join it. The gradient then flattens out (to about 0.013) for the 14 km of river course through the Du Toit's Kloof Valley, where the site is located at an altitude of 370 m a.m.s.l. The confluence of the Elands with the mainstream constitutes a geomorphological segment boundary, upstream of which the Molenaars River exhibits physical features typical of a mountain stream (Wadeson 1996). Downstream of its confluence with the Elands, the Molenaars is a fifth-order river (although classed by some authors as fourth-order - Table 2.4), typical of a southwestern Cape foothill river, *sensu* Harrison (1965). From the Elands confluence to the end of the Du Toit's Kloof Valley, the foothill zone of the Molenaars River is divided into four distinct geomorphological reaches, within one of which the site is located. This section of the river, especially from the Huguenot Tunnel to just downstream of the Klip River (Figure 2.8), is relatively broad, with gentle slopes underlain by Cape granite (Carter 1988, cited in Ractliffe and Brown 1994). Further downstream, the valley is deeply incised and narrow, and is characterised by steep sandstone slopes.

The river channel at the study site is alluvial, typically single with occasional multiple channels, fairly wide and well defined (as defined in Gordon *et al.* 1992). The reach is of the pool-riffle type (Rowntree and Wadeson 1999; King and Schael 2001). The bed is moderately gentle in gradient at 0.013 (Wadeson 1996; Table 2.4), with a heterogeneous substratum dominated by multiple boulder-cobble layers, but also with patches of gravel and sand (Section 6.3.4, Figure 6.26). Several bedrock outcrops occur at the site (some a result of valley side scree) and there are occasional mid-channel cobble bars, some vegetated with indigenous fynbos. The banks forming the active channel comprised a combination of palmiet and mineral substrata from sand to bedrock. Physical biotope heterogeneity and hydraulic diversity are high, and biotopes include pools, riffles, runs, transitional biotope patches and backwaters (Chapter 6).

Riparian and instream vegetation

Most of the Molenaars tributary streams are closed-canopied (Ractliffe and Brown 1994), while others like the Krom and Elands have largely open canopies. Longitudinal stands of wetland vegetation are associated with the extensive network of seepage lines on the mountain slopes, through which water is additionally contributed to the mainstream. At the study site, the riparian canopy is largely open, comprising mostly indigenous mountain fynbos (Table 2.3). Species include Restionaceae, Cyperaceae and small trees like *Salix mucronata*. Alien species have invaded the length of the riparian zone upstream of and at the site, in particular *Acacia mearnsii* and *A. longifolia*. Marginal and instream stands of indigenous *Prionium serratum* occur at the site.

Water chemistry

Baseline water chemistry conditions at the Molenaars site are derived from pilot data (Table 2.10), compared, where possible, with seasonal, long-term water chemistry data recorded at weir H1H018 (DWAF 1991c, cited in Ractliffe and Brown 1994), as well as limited summer data collected by Ractliffe and Brown (1994) for sites upstream and immediately downstream of the site. Examination of the historical DWAF data revealed clear seasonal differences in water quality.

The daily water temperature was about 21.0 °C at the time of summer pilot sampling. The water was mildly acidic to neutral, at a pH of 6.8. This value exceeded the median background pH of 6.0 obtained for least-impacted foothill zones in the region, but fell within the overall regional range of 4.0-7.2 units (Dallas *et al.* 1998). Lower pH values occur in the river in winter, due to increased leaching of organic acids from fynbos (Ractliffe and Brown 1994). Summer average TA was 0.095 mEq ℓ^{-1}. Conductivity was low at about 3 mS m^{-1}, and TDS values were correspondingly low at an average of 27.77 mg ℓ^{-1}. Both figures are just less than the background median values of 3.1 mS m^{-1} and 32.0 mg ℓ^{-1}, respectively, for least-impacted foothill zones (Dallas *et al.* 1998). Conductivities are similar in summer and winter, while TDS concentrations tend to be lower in winter (Ractliffe and Brown 1994). The summer concentrations of major cations and anions were all low, with sodium and chloride dominant, at 0.172 mmol ℓ^{-1} and 0.156 mmol ℓ^{-1}, respectively. Oxygen

levels were high, at 8.6 mg ℓ^{-1} (95.6% saturation). Ractliffe and Brown (1994) could not detect marked seasonal trends in oxygen concentrations, with high levels recorded year-round. TSS levels were extremely low in March 1994, at 0.001 mg ℓ^{-1}, falling well below the regional background median TSS concentration for least-impacted foothills (Dallas *et al.* 1998) and corresponding with high water clarity. Ractliffe and Brown (1994) recorded summer TSS ranges within the foothill zone of 0.70-3.05 mg ℓ^{-1}. Turbidity levels typically increase markedly as a result of floods during winter. Nitrate concentrations during the pilot survey, at an average of 15.885 μmol ℓ^{-1}, indicated mild nutrient enrichment (Dallas and Day 1993). Ractliffe and Brown (1994) recorded similar summer values and lower winter maxima. Examination of DWAF data also revealed summer peaks in nutrient concentrations, principally attributed to the effects of upstream trout farming. March 1994 nitrite and phosphate concentrations were fairly low at 0.210 μmol ℓ^{-1} and 0.923 μmol ℓ^{-1}, respectively. Winter nitrite and phosphate levels are typically lower than summer values (Ractliffe and Brown 1994). Ammonium levels were below detection limits for the pilot study, but a summer range from 1.8-9.1 μmol ℓ^{-1} for the foothill zone was found by Ractliffe and Brown (1994). The summer concentration of silicon was high at 6.475 μmol ℓ^{-1}.

There was some silt deposition at the site, but the surfaces of the substratum were virtually free of algal growth at the time of the pilot survey. Some patches of algae were evident, however, at other times during the dry season (pers. obs.) and species records are available for upstream and downstream reaches. High summer and winter algal densities have been observed along the foothill zone, possibly in response to increased availability of nutrients (Ractliffe and Brown 1994). A further indication that the river is mildly enriched at times is provided by the growth of heterotrophic slimes in slow-flowing areas (Ractliffe and Brown 1994; pers. obs.). From these data, as well as SASS assessments below, it is clear that the river is in good condition in terms of its water quality, although mild nutrient enrichment has been occurring for more than two decades.

Aquatic biota

Some 129 macroinvertebrate taxa, at species level and above, have been historically recorded along the Molenaars River (Ractliffe and Brown 1994) and 32 families were recorded from the site during the pilot survey (see Appendix 2.2 for taxon abundances). A characteristic, particularly diverse, foothill insect-dominated assemblage inhabits the site; nematodes, oligochaetes and planarians as the main non-insect taxa. Sensitive taxa indicative of least impacted upper rivers observed during the pilot survey included: Helodidae; Athericidae; Leptophlebiidae, Teloganodidae; Notonemouridae; Leptoceridae; Pyralidae and Corydalidae. There were also a number of undescribed species, including a new Gondwanaland relict trichopteran (Tribe Leucotrichiini). Invertebrate abundances are variable and may reach exceptional densities of 120 000 individuals m^{-2} (Ractliffe and Brown 1994). Primary consumer productivity has been rated far in excess of rates expected for oligotrophic southwestern Cape systems (Ractliffe and Brown 1994). Population

explosions of opportunist species are known to occur in summer, probably as a response to warm summer temperatures, low flows, nutrients, and high algal production (Ractliffe and Brown 1994; this study).

Invertebrate SASS scores previously recorded from the river compare favourably with, and are within the upper range for, SASS scores reported from relatively undisturbed rivers elsewhere in the southwestern Cape (Ractliffe and Brown 1994). SASS scores for the foothill zone in summer ranged from 160-196, number of taxa from 20-23, and ASPTs from 7.6-8.7; winter scores were lower.

Eleven fish species are known to inhabit the Molenaars River system (Ractliffe and Brown 1994). Three common, indigenous fish species have been recorded from the Molenaars River, namely: *Galaxias zebratus*, *Sandelia capensis*, and *Anguilla mossambica* (longfin eel) (Ractliffe and Brown 1994). Two Red Data species, *Pseudobarbus burchelli* (Burchell's redfin) and *Barbus andrewi* (witvis) inhabit the Elands River and the mainstream Molenaars, respectively. Alien fish include the widespread *Oncorhynchus mykiss* and *Micropterus dolomieu*. A further four alien species have been recorded from the river downstream of the valley: *Lepomis macrochirus* (bluegill sunfish), the Mozambique and banded tilapias *Oreochromis mossambicus* and *Tilapia sparrmanii*, respectively, and *Micropterus salmoides*.

Status of conservation and water resource development

The Molenaars River is a designated Special Standards River, although it exhibits ecosystem alteration, including invasion by alien biota and localised water pollution (Ractliffe and Brown 1994). It is still recognised as having a high conservation importance, however, and some of its tributaries (e.g. Tierkloof Stream) were rated of exceptionally high importance (Ractliffe and Brown 1994). The abiotic and biotic conservation statuses of the river reach encompassing the site were calculated as 62.4% and 64.6%, respectively, indicating that the reach is moderately modified. Although there has been a loss and change of natural habitat and biota, basic ecosystem functioning appears predominantly unchanged. The river has an unusually long foothill zone, characterised by an exceptional invertebrate biodiversity, as well as by a high number of riverine wetlands scarce elsewhere in the southwestern Cape.

Presently, the catchment is largely undeveloped in terms of its water resources, and there are no major impoundments on the mainstream or tributaries. Several sites on the river have been investigated for water storage within the Western Cape System Analysis (DWAF 1994, 1997).

2.4.3 Du Toits site

The location of the study site on the Du Toits (or Du Toit's) River (1:50 000 topographical map 3319CC Franschhoek, 2nd ed. 1977, partially revised 1987) is indicated in Figure 2.8. Site longitude and latitude are given in Table 2.2, while a brief site description is given in Table 2.3. Natural river characteristics at the site are shown in Plate 3.5.

Catchment characteristics and hydrology

The Du Toits site falls within WR90 quaternary subcatchment H60B (DWAF 1997), for which the total subcatchment area is the second smallest of the four study sites at 46.02 km^2 (Table 2.2). The subcatchment receives a MAP in the order of 1445 mm a^{-1}, with a corresponding MAE (S-Pan) of 1288 mm a^{-1} (DWAF 1997). Runoff figures are given in Chapter 4, along with a description of the hydrological regime.

The perennial Du Toits River forms part of the Breede system, and is essentially a tributary of the Riviersonderend River (Section 2.4.4), truncated by Theewaterskloof Reservoir. The river has its source in the Middagkransberg and Franschhoek mountains, at an altitude of about 1500 m. It is fed by several seasonal mountain streams and the Paardekloof, Perdekloof and Kafferskloof Rivers are the main perennial tributaries forming the headwaters (Figure 2.1). Downstream of the confluence of the latter tributaries, the mainstream Du Toits forms a short (*c.* 13.4 km), third order river (Table 2.4; some authors have classed it as second order) that flows through the steep-sided, narrow Franschhoek Pass. The arterial road linking Franschhoek and Villiersdorp runs alongside the river through the pass. Along this course, the Du Toits receives perennial flow contributions from the Joubertsgat River and several other tributaries (Figure 2.8). A hydrological gauging weir, DWAF weir H6H007, is situated within the study site, at Purgatory Outspan (Table 2.2; Figure 2.8). The weir is located immediately downstream of the confluence of an unnamed perennial tributary that arises in the Baviaans Kerk 2 region, with the mainstream. Distance from source to the site is roughly 11.3 km and altitude, 370 m a.m.s.l. The river finally passes under a road bridge before flowing through a large palmiet-dominated wetland, designated a Natural Heritage Site, and into Theewaterskloof Reservoir (Tharme and Brown 1994; Figure 2.8).

The largely mountainous upper subcatchment is a designated Mountain Catchment Area (MCA) (Mr Steyn, Franschhoek Municipality, pers. comm.), and much of it is located within the protected 1759 ha Mont Rochelle Nature Reserve. As a result, it is largely undeveloped, with land use primarily limited to recreation. Several scattered patches of alien vegetation, including *Pinus* spp., occur in the MCA, with the area of alien vegetation with a density greater than 25% estimated as 3.5 km^2 as at 1993 (DWAF 1997). The majority of the area is covered with mountain fynbos and there are no commercially afforested or agricultural areas. The last land-use activities do occur in adjacent subcatchments (DWAF 1997). The middle and lower subcatchments of the Du Toits River are largely encompassed by the Hottentots Holland Nature Reserve, and a section of the Boland Hiking Trail runs close to the river for a short distance. There are camping facilities alongside the river in its upper reaches and upstream of the lower-reach wetland. The closest town to the study site is Franschhoek, situated on the southwestern side of the Franschhoek Mountains, so there is no urban development in the catchment.

Geomorphology

The upper river has a steep gradient and exhibits physical features characteristic of the mountain stream zone of a southwestern Cape river, including a narrow, single channel dominated by shallow riffle and short

cascade sections interspersed with deep bedrock-bottomed pools. Further downstream, in the reach including the study site and DWAF weir, the Du Toits transforms into an alluvial, single thread foothill river (Table 2.3) of plane-bed reach type (Rowntree and Wadeson 1999). The gradient is somewhat gentler (0.04) and the substratum dominated by subangular to rounded small cobble, in addition to gravel, large cobble and small boulders (Section 6.3.4, Figure 6.26). An assessment of river bank composition showed dominance by sand and woody shrubs, with small boulders also in relatively high proportions.

Riparian and instream vegetation

The Du Toits River has a largely open riparian canopy of indigenous mountain fynbos along much of its length and at the study site, although the canopy tends to be closed along its headwater streams. There are no visible signs of removal of indigenous riparian vegetation or encroachment of exotic species at the site. Although no formal survey has been made of the distribution and composition of the riparian vegetation, some of the dominant species identified in Tharme and Brown (1994) from reaches upstream of the study site are: *Metrosideros angustifolia* (lance-leaved myrtle)*; Podalyria calyptrata; Euryops* sp.; *Brabejum stellatifolium* (Cape wild almond)*; Erica caffra;* and *Myrica serrata.* The macrophyte *Prionium serratum* occurs instream and along the channel margins at the site.

Water chemistry

Dry season pilot data were used to gain an understanding of natural, dry-season water chemistry (Table 2.10). There is no published literature on historical seasonal chemistry, although there are historical DWAF chemistry records for the study site (DWA 1990; see Table 5.6). Pilot measurements were all within the range of readings recorded by DWAF, for those variables common to both data sets.

The instantaneous, summer water temperature was about 22 °C, with a range from 21.0 °C to a maximum as high as 27.0 °C. The water was acidic, at a pH of 5.7, a value between regional median pH values of 5.5 and 6.0 obtained for least-impacted mountain stream and foothill zones, respectively (Dallas *et al.* 1998). Average TA was low at 0.065 mEq ℓ^{-1}. Conductivity was very low at about 3 mS m^{-1}, and TDS values were correspondingly low at an average of 21.44 mg ℓ^{-1}. Both figures are just below historical averages, and just less than the background median values of both least-impacted mountain stream and foothill zones of the same region (Dallas *et al.* 1998). The concentrations of major cations and anions were low, with sodium and chloride constituting the dominant ions, at 0.201 mmol ℓ^{-1} and 0.256 mmol ℓ^{-1}, respectively. Oxygen levels were near saturation. TSS figures were negligibly low, corresponding with high water clarity during summer, and well below the regional background median TSS concentration for least-impacted mountain stream and foothill zones (Dallas *et al.* 1998). Nutrient levels, specifically nitrates (0.468 μmol ℓ^{-1}), nitrites (0.063 μmol ℓ^{-1}) and phosphates (0.093 μmol ℓ^{-1}) were low, with ammonium below detection limits. Such nutrient concentrations are typical of least-impacted upper rivers (Dallas and Day 1993). Summer silicon

concentrations were about 0.865 μmol ℓ^{-1}. Invertebrate SASS results further indicated that water quality was excellent (Tharme and Brown 1994).

Aquatic biota

The pilot invertebrate data for the dry season showed a total of 28 families and higher taxa inhabiting the site (Appendix 2.2). The assemblage was insect-dominated, with nematodes and oligochaetes as the main non-insect taxa. Sensitive taxa indicative of least-impacted upper rivers included: Helodidae; Athericidae; Leptophlebiidae; Teloganodidae; Notonemouridae; cased trichopterans, including Leptoceridae; and Corydalidae. There were no known exotic aquatic macroinvertebrates (Tharme and Brown 1994).

A once-off SASS assessment of the headwaters and mountain stream zones of the Du Toits, in March 1994, indicated a range of 16-20 macroinvertebrate families and higher order taxa; there is no species list for the river (Tharme and Brown 1994). The SASS Scores ranged from 171-133 and ASPTs from 8.3-8.6. The results were well within the ranges considered typical of near-pristine, southwestern Cape mountain stream and foothill zones. Consequently, the river could be classed as being in excellent biological condition.

The Cape galaxias has been recorded from the Du Toits River (Tharme and Brown 1994). Although not recorded from the river, the endangered Berg River redfin, *Pseudobarbus burgi* (Family Cyprinidae; Skelton 1993) possibly inhabits it (Skelton 1987). There were no reported alien fish species (Tharme and Brown 1994).

Status of conservation and water resource development

Although currently not designated with respect to conservation importance, the Du Toits River is likely to be of high importance as much of the catchment is located within conservation areas, and the river is in a largely natural condition. Tharme and Brown (1994) estimated the abiotic conservation status of the river's upper reaches as Class 2, indicating that the functioning of the riverine ecosystem is essentially still natural, although a small change in natural habitats and biota may have occurred. Existing water abstraction was given as the main reason for not allocating the river a Class 1 abiotic conservation status. The biotic present conservation status for the upper river was calculated as extremely high (Class 1), where the reach has 100% of its potential value, and is natural and unmodified.

As the Du Toits River flows into Theewaterskloof Reservoir (Figure 2.8), it is a contributor to the Theewaterskloof Scheme (Tharme and Brown 1994). Although there are no farm dams or major impoundments on the Du Toits River or any of its tributaries (Tharme and Brown 1994; DWAF 1997), Franschhoek Municipality abstracts water from two locations on the river system, both some distance upstream of the study site, principally for domestic use. The first abstraction point is a diversion weir on the Paardekloof tributary (Figure 2.8) from which the municipality had a year-round limited water allocation;

records of abstraction volumes are not kept (Tharme and Brown 1994). The second abstraction weir is located on the mainstream approximately 100 m downstream of the Kafferskloof confluence. Pumped run-of-river abstraction occurs during the summer months, from November until March or April (Tharme and Brown 1994). Although Franschhoek Municipality is currently entitled to pump a maximum of 667.2 kℓ day^{-1} all year round, no records of abstracted water volumes are available; in March 1994, Tharme and Brown (1994) recorded an instantaneous abstraction of 67% of total river flow.

2.4.4 Riviersonderend site

The Riviersonderend study site (1: 50 000 topographical sheet 3419 AA Grabouw, 2nd ed. 1979, partially revised 1987) is located just upstream of Theewaterskloof Reservoir (Figure 2.8). Site co-ordinates are provided in Table 2.2, and a brief comparison with other sites is made in Table 2.3. The natural character of the site is illustrated in Plate 3.7.

Catchment characteristics and hydrology

The total catchment area of the Riviersonderend River upstream of the study site is represented by WR90 quaternary subcatchment H60A (DWAF 1997). At 38.57 km^2, it has the smallest area of the four study catchments (Table 2.2). The total Riviersonderend Basin has an area of 494 km^2. The MAP of the subcatchment is 2314 mm a^{-1}, with a corresponding MAE (S-Pan) of 1175 mm a^{-1} (DWAF 1997). The virgin and present-day MARs at the study site are given in Chapter 4, where site hydrology is described. The perennial Riviersonderend forms part of the Breede River system. The linkages of several of its tributaries with the mainstream, including the Du Toits River, are interrupted by Theewaterskloof Dam (Section 2.4.3).

The river rises in the western Groot Drakenstein Mountains near Landdroskop, at an altitude of about 1590 m a.m.s.l. The Riviersonderend is joined by two main perennial tributaries in its upper reaches, Boegoekloof tributary and another arising near Victoria Peak. It flows in a southeasterly direction through Riviersonderendkloof for approximately 15 km, as a fourth order river, before it enters Theewaterskloof Reservoir, at 300 m a.m.s.l. The site is located upstream of the reservoir, at an altitude of 350 m. Downstream of the impoundment, the Riviersonderend flows eastwards through the Donkerhoekberge, which are situated at the southwestern limit of the Riviersonderend Mountains. The Riviersonderend Mountain range extends in a broad east-west band, receiving considerable, though unpredictable, orographic summer precipitation from onshore southeasterly winds along the south coast. However, most rainfall is received in winter, from northwesterly frontal systems. The river is fed by runoff from the southern slopes of the Riviersonderend Mountains for some 90 km, before flowing north-east and then eastwards before joining the Breede River west of Swellendam.

The natural vegetation of the upper Riviersonderend Catchment comprises mesic and xeric fynbos (Ractliffe *et al.* 1996). In the vicinity of Theewaterskloof Reservoir and in the river valley downstream of it, there is

some renosterveld on areas of Bokkeveld shales. Above Theewaterskloof Dam, the catchment is largely unimpacted by human disturbance, as it is mostly located within the Hottentots Holland Nature Reserve, but a limited afforestation with commercial pines is apparent (as at 1993) (Ractliffe *et al.* 1996; DWAF 1997). Only occasional *Pinus* are present on the mountain slopes flanking the site. There are no areas within the MCA with a density of alien vegetation greater than 25%, and no area of the upper catchment under irrigation or urban development (DWAF 1997). Physical impacts at the site, located *c.* 11.2 km from the river's source, are the now-closed DWAF gauging weir, H6H008, and a section of the Boland Hiking Trail. A wooden bridge is located just downstream of the gauging weir, and a dirt road ends near it. Agriculture is the major land use in the catchment downstream of Theewaterskloof Dam and, with flow regulation, has resulted in significant detrimental changes to the middle and lower river system (Ractliffe *et al.* 1996).

Geomorphology

The source and upper reaches of the river, including the study site and Riviersonderend Mountains, cut through predominantly TMS sandstones and quartzites of the Cape Fold Mountains (Lambrechts 1979). A macro-reach analysis revealed that four of a total of 12 geomorphological reaches identified for the Riviersonderend occur upstream of the impoundment (Ractliffe *et al.* 1996). The average gradient for the upper river is 32 m km^{-1}. The mountain stream zone (Reach 4), of altitude 480-320 m and length 5 km, includes the study site, of approximate gradient 0.02. Geologically, in this alluvial, pool rapid reach (Rowntree and Wadeson 1999), the river passes through shale, with thin bands of sandstone, tillite, grit and conglomerate (Ractliffe *et al.* 1996). The river bed comprises a substratum of predominantly small boulders with several bedrock outcrops instream and along the banks, as well as cobble, gravel and small amounts of sand (Section 6.3.4, Figure 6.26). The major biotopes are riffles, runs and large deep pools, with occasional backwaters and cascades (Chapter 6). Alongside the wetted channel the banks comprised mostly bedrock and medium-sized boulders.

Riparian and instream vegetation

Riparian vegetation at the site is virtually entirely natural, comprising typical elements of mountain fynbos, including *Brabejum stellatifolium* and *Metrosideros angustifolia* trees. A few young pine trees have invaded the riparian belt. *Prionium serratum* occurs in small areas along the channel margins at the site, becoming increasingly dense near the upstream end of Theewaterskloof Reservoir. Instream, *Isolepis digitata* is highly abundant, especially on the tops of immovable boulders and bedrock.

Water chemistry

Historical winter and summer water chemistry data are available from records taken at the DWAF gauging weir, H6H008, and those data from the period 1977-1992 were analysed by Ractliffe *et al.* (1996). The data obtained during the pilot study also were used to gain a better understanding of natural, dry season

concentrations (Table 2.10); the following description pertains to summer conditions unless otherwise specified.

The March pilot daily water temperature was between 19.0 and 21.0 °C. The water was highly acidic, with a pH of 4.5. According to historical data, the median pH is below 4.7 in both summer and winter, figures well below the median background pH of 5.5 for least-impacted mountain stream zones (Dallas *et al.* 1998). Median pH values tend to be lower in the winter, consistent with greater leaching of acidic polyphenols from catchment fynbos (Midgeley and Schafer 1992). An average summer TA of 0.065 mEq ℓ^{-1} closely matched the historical median value. Conductivity was low, at about 3 mS m^{-1}, and TDS was similarly low, at 22.31 mg ℓ^{-1}. Both figures approximated background median values calculated by Dallas *et al.* (1998) for least-impacted mountain stream zones, and compared well with long-term summer and winter median conductivities recorded at well below 5 mS m^{-1}. Summer concentrations of major cations and anions were low and within the observed historical range. Sodium and chloride were the dominant ions, at 0.161 mmol ℓ^{-1} and 0.201 mmol ℓ^{-1}, respectively. According to historical records, median concentrations of chloride, sodium and magnesium are marginally higher in summer than winter, although seasonal differences are not marked. For the other major ions, summer and winter concentrations are similar. Oxygen levels in March 1994 were high at about 8.8 mg ℓ^{-1} (an average saturation of 96%). TSS levels were negligible at the site, well below the regional background median TSS concentration for least-impacted mountain stream zones (Dallas *et al.* 1998), and corresponded with high water clarity. Nutrient levels, specifically nitrates (0.135 μmol ℓ^{-1}), nitrites (0.260 μmol ℓ^{-1}), and soluble reactive phosphates (0.668 μmol ℓ^{-1}), were very low; ammonium levels were below detection. Such nutrient concentrations are typical of unimpacted upper rivers in the region (Dallas and Day 1993). The concentration of reactive silicon was 0.525 μmol ℓ^{-1}. Although there appeared to be occasional mild nutrient enrichment of the river at the site on the basis of historical data, such enrichment was not apparent during the present study.

Aquatic biota

The pilot sampling trip revealed a total of 28 invertebrate families dominated by insects, with non-insect taxa being planarians and oligochaetes (Appendix 2.2); see also Ractliffe *et al.* (1996). Sensitive taxa indicative of least-impacted upper rivers included: Helodidae; Athericidae; Leptophlebiidae, Teloganodidae; Notonemouridae; several trichopterans, including Leptoceridae; Pyralidae; and Corydalidae. *Potamonautes perlatus* (Cape river crab) a common, hardy inhabitant of Western Cape rivers occurred at the site (Ractliffe *et al.* 1996).

Five indigenous fish species have been recorded from the river downstream of Theewaterskloof Dam, namely: *Pseudobarbus burchelli* (Burchell's redfin); *Barbus andrewi* (Breede witvis); *Sandelia capensis*; *Galaxias zebratus*; *Anguilla mossambica* (longfin eel) (Ractliffe *et al.* 1996). The first two species are rare and vulnerable, respectively (Skelton 1987, 1993). It is not known whether these or other species occur at

the site. Similarly, seven alien species have been recorded from Theewaterskloof Dam and below, and may be present in the upper river: *Oreochromis mossambicus*; *Tilapia sparrmanii*; *Micropterus dolomieu*; *Micropterus salmoides*; *Lepomis macrochirus*; *Tinca tinca* (tench); and *Cyprinus carpio* (common carp).

Status of conservation and water resource development

Ractliffe *et al.* (1996) assigned a high conservation importance to the Riviersonderend River. The reach that includes the study site was attributed a high overall conservation status of 96%, with an abiotic conservation status of 96% and a biotic conservation status of 95%. These scores place the site in a Class 2 conservation-status class, indicating that the functioning of the riverine ecosystem is essentially still natural.

There are no existing or proposed water resource developments, including farm dams, above or at the study site (DWAF 1997). Downstream reaches of the river are regulated by a major water-resource development, Theewaterskloof Dam, operational in 1980 and with a 482 x 10^6 m^3 storage capacity (Ractliffe *et al.* 1996). The reservoir is a source for the Riviersonderend-Berg-Eerste River Government Water Scheme, an interbasin water transfer project that has a substantial effect on the hydroecology of the lower river (Ractliffe *et al.* 1996).

3. STUDY METHODOLOGY

3.1 STUDY DESIGN AND PROCEDURES FOR FIELD IMPLEMENTATION

3.1.1 Basic study design

As low flow is a natural form of physical disturbance (Section 1.4), the main study aimed to differentiate among biophysical responses to natural low flows and more extreme, manipulated discharge reductions (Townsend 1989; Townsend *et al*. 1997a; Section 1.2). As Power *et al*. (1988, p. 458) observed, "Adequate sampling of natural flow environments…will set the stage for experimental studies of biotic responses to flow". In this thesis a combined approach was adopted, with acknowledgement of the various limitations imposed by experimental study scale (Fisher 1987; Fisher and Grimm 1988; Minshall 1988; Brooks and Boulton 1991; Matthaei *et al*. 1997). Biophysical responses under both natural and experimental conditions were studied alongside one another, and at multiple sites with contrasted flow disturbance regimes. Hildrew and Giller (1994) identified a need to move into such a phase of larger-scale field experimentation, to better understand the relationships among disturbances, instream habitat factors and biotic response, although Lake *et al*. (1989) cautioned that it might not be feasible to execute disturbance experiments at the larger scales at which disturbance might influence biota.

The statistical power to detect an environmental impact, isolating it from the noise generated by natural spatiotemporal variability, is constrained by three main factors: (1) the variability of the data; (2) the magnitude of the supposed impact; and (3) the number of independent (serially uncorrelated) sampling events (Osenberg *et al.* 1994). For example, if the size of an anthropogenic impact is small relative to natural variability, it will be difficult to detect with any degree of confidence. This is of particular relevance in this study, where flow reduction is a natural phenomenon that can be exacerbated by manipulation. Osenberg *et al.* (1994) acknowledged that while temporal coherence is influential in potentially altering estimation of impact (outside of within-site sampling variability and error) there exists little guidance on the requisite sampling frequency, intensity or parameter selection for field experiments of ecological perturbations. Parameters based on populations and physical-chemical information generally tend to provide less statistical power (i.e. have relatively low probabilities of demonstrable results) than individual-based ones (e.g. body size) (Osenberg *et al.* 1994). Chemical and physical parameters were considered more amenable to impact detection than population-based ones, however, as they tended to be less inherently variable and their sensitivity to local conditions is relatively low (cf. population parameters such as density). Population parameters tended to be more responsive to impact effect, but had much greater natural variability, than chemical and physical parameters. Niemi *et al.* (1993) also observed that certain chemical

and biological variables possessed higher explanatory power than others in evaluating a specific disturbance. A combination of biophysical variables was employed in this study, enhancing as far as feasible the likelihood of impact detection.

Foundation of the low flow study

The low flow field study was basically structured as an extended Before-After Control-Impact (BACI) design with paired sampling (BACIP). Discussions of BACI designs, including their underlying assumptions, are provided in Bernstein and Zalinski (1983), Stewart-Oaten *et al*. (1986), Underwood (1993, 1994) and Osenberg *et al.* (1994). Simply, the putative effect of an impact at a site is assessed by comparing the ecological parameter(s) of interest at the site with that at an unimpacted site (control), through simultaneous, paired sampling several times both before and after occurrence of the impact (Figures 3.1(a)-(d)). In order to have a detectable effect, the disturbance should cause more change in the impact location than occurred at the control location (Underwood 1994; Osenberg *et al.* 1994).

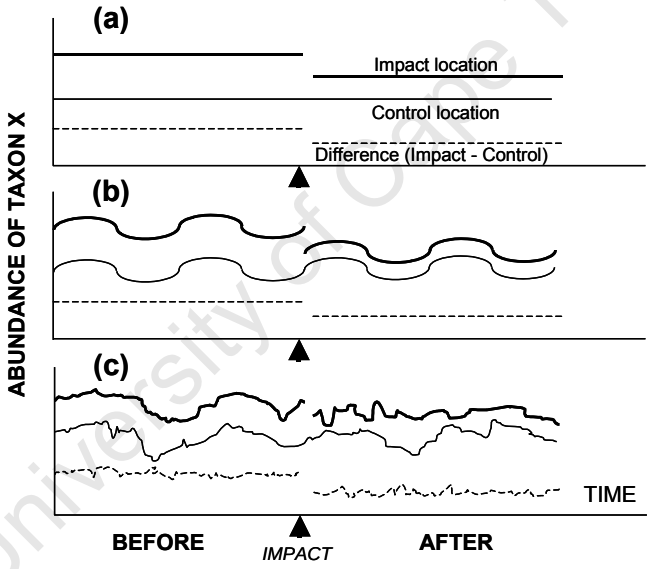


Figure 3.1 (a-c) Hypothetical abundances of "taxon X" at impact and control locations, and the difference of the abundances, as functions of time, in three versions of assessment of an impact (e.g. flow reduction) (adapted from Stewart-Oaten *et al.* 1986). (a) Simplistically, abundance is constant at each location (though possibly different for different locations) except for a decrease at the impact location at the start of the impact. (b) More realistically, abundances fluctuate (e.g. seasonally), but the difference in abundance remains constant, except following the impact. (c) Realistically, abundances fluctuate, in synchrony and separately due to random influences (e.g. drift).

The field layout employed was aimed, as far as possible, at avoiding potential sources of confusion in experimental design (Hurlbert 1984; Stewart-Oaten *et al*. 1986; Resh *et al*. 1988; Underwood 1993). It particularly addressed the issue of pseudoreplication (i.e. the use of inferential statistics to test for treatment

effects with data from experiments where treatments are either not replicated, though samples may be, or replicates are not statistically independent; Hurlbert 1984; Carpenter 1990).

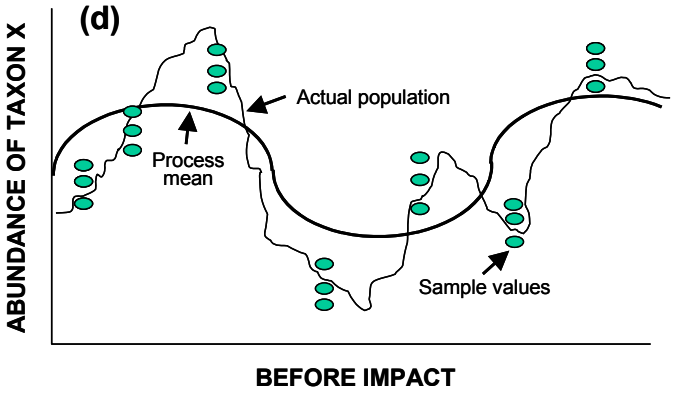


Figure 3.1 (d) The three functions to be distinguished in the characterization of the differences between the Control and Impact locations of Figure 3.1a-c (adapted from Stewart-Oaten *et al.* 1986). The smooth curve represents the true mean abundance of the population.

Use of a BACI design enabled impact detection, revealing whether the difference between response measures at a control site and an impact site changed once flow treatment commenced, with sampling replicated in time (Stewart-Oaten *et al*. 1986). The importance of taking invertebrate control samples concurrently with experimental ones was especially recognised, in that natural assemblages may exhibit continual, sometimes large changes in species abundances and composition over short periods (Lake and Doeg 1985; Doeg *et al*. 1989; Armitage and Petts 1992). Minshall (1988) emphasised that the dynamics of the system and study organisms should dictate the time scale for a sampling strategy. Both factors were considered in the selection of the temporal frequency and period of sampling. Temporal extension of the experiment, closely tied to the different hydrologic phases (Stanley and Fisher 1992), was achieved by sampling during flow reduction, as well as before and after impact.

Spatial extension of the basic design was achieved through replication of flow treatments, with replicated locations (two per site reach) at multiple sites (four, one on each study river; Section 2.3). At each site, the upstream of the two locations acted as a 'control', tracking natural changes in site biophysical conditions. The downstream ones were the experimental ('impact') locations, in that they had various proportions of flow experimentally diverted from them. While flow reduction treatments were assigned randomly to three sites, the fourth site acted as a control treatment (no flow diversion), to account for any unanticipated effects of field procedures, as well as to track within-reach spatiotemporal variability; hence, at the control site, both 'control' and 'impact' locations reflected natural flow conditions. In this study, the potential statistically confounding error of consistent positioning of control locations upstream of experimental ones (Resh *et al*. 1988) was dealt with as far as possible, firstly by establishing through a pilot survey (Section 2.3) that

upstream and downstream locations within the same reach were similar in dry-season biophysical character and secondly, by having a control site (Elands River). Controls downstream of the impacted locations would likely have been subject to any effects of invertebrate drift, or other physical or chemical changes associated with upstream flow-related impacts, rendering them unusable. The experimental layout provided for both multivariate and univariate analyses of flow-related assemblage change (Underwood 1993).

Figures 3.2-3.5 schematically illustrate the field layout adopted at each site. A 60-m long control location, encompassing the full width of the active channel, was delineated upstream of a predetermined flow diversion point, while a 60-m long impact location was located no further than *c.* 80 m downstream of it. The total length of river for each location, for each site, was within 10-14 times the average width of each river, ensuring that each location included a series of at least two riffle-run or equivalent geomorphological sequences (Bovee and Milhous 1978; Brizga 1998). The locations were situated in similar, though not identical, positions to original pilot locations to ensure they remained hydrologically and biophysically comparable (as established by pilot study results; Section 2.3). They were also situated within the domain of permissible extrapolation from flow gauges (Poff *et al*. 2006a), at a maximum distance from stations of 200 m (Figures 3.2-3.5). Although it was preferable to use sites at which flow gauging had been long-term (McMahon and Finlayson 2003) and was ongoing, this was only feasible for the Elands and Molenaars sites (Table 2.2; Section 3.2). Areas in close proximity to diversion structures were excluded from sampling, to avoid any localised backwater effects.

3.1.2 Structure of the temporary diversion weirs

Temporary diversion weirs, designed by the author in consultation with hydraulics experts, were constructed and later dismantled by DWAF Hydrology Division, Worcester. Although it would have been preferable to establish a flow diversion structure at the Elands site (Figure 3.2) to control for the physical presence of a diversion weir, and through which the total discharge of the river could pass unimpeded, this was not feasible due to cost and manpower constraints (M. Acker, DWAF Hydrology Division, Worcester, pers. comm.). It also was not possible to repeat the diversion of flow over more than one summer. Plate 3.1 illustrates the general features of the Elands 'impact' location, where no flow was diverted. For the other sites, river water was diverted from an existing gauging weir or temporary sandbag weir through a series of PVC pipes located within the main river channel, from immediately downstream of the control location to the end of the impact location (Figures 3.3-3.5). Diverted water was re-introduced immediately downstream of the impact location directly from pipe openings.

The form of the flow diversion structure was necessarily site-specific, as illustrated in Figures 3.3-3.5 and Plates 3.2-3.4. Originally, at the Du Toits and Riviersonderend sites, it was intended to use the existing gauging weirs as points of diversion. However, this was not possible in either case (see Section 2.3.1), so sandbag weirs were constructed at the upstream ends of the experimental locations within these reaches. The entire channel bottom width was first sealed off with black plastic sheeting, on top of which rows of

sandbags were stacked. Offtake pipes were set within the sandbag wall, and then extended along the bottom of the river channel (Figures 3.4 and 3.5; Plates 3.3 and 3.4). Short sections of pipe were incorporated in the sandbag walls to ensure that the non-diverted portion of flow was evenly distributed within the main channel immediately downstream of each weir. As the locations upstream and downstream of the gauging weir on the Molenaars River fulfilled all criteria (Table 2.1), and given the relatively high dry season discharge of this river (Table 2.4), the existing weir was used as the offtake point (Figure 3.3; Plate 3.4). Two large pipes were fitted to the weir scour gate using a customised welded plate. Ongoing, automated flow gauging at the site enabled a check to be kept of the proportion of flow being diverted during construction. For this site, an insufficient length of pipe was available to divert the water over the entire length of the impact location, so only *c.* 45 m of river length were affected by flow reduction (Figure 3.3).

In all cases, construction of the diversion weirs followed a structured set of procedures aimed at minimising human disturbance that might have detrimentally affected the biota, physical habitat or chemistry. Establishment of each weir was done within a period of at most three days, and dismantlement took place within a matter of hours. Sand for sandbags for the Du Toits and Riviersonderend diversion weirs was clean, dry river sand excavated immediately downstream of the sites; it was returned to the excavation areas once the weirs were dismantled. Construction work on the weirs was done from the banks or instream bedrock/boulders and walking through the wetted river bed was avoided. Diversion pipes within the wetted channel were elevated out of the water.

3.1.3 Nature of the experimental flow reductions

A graded series of discharge reductions (experimental treatments) was applied to the four sites, where each reduction represented a proportion of the site's natural instantaneous low flow (and a 'pulse disturbance', *sensu* Bender *et al.* 1984; Section 1.4.3). Assignment of flow reduction percentages to particular sites was random and approximate. Exact percentage reductions in discharge were not feasible, due to the difficulties associated with construction and operation of the temporary weirs. However, the numbers and diameters of pipes of each of the three diversions were adjusted until an approximate reduction in the series 0% (Elands control treatment), 30%, 80% and 85% of natural dry-season low flow was achieved (Table 3.1). Calculations of actual proportions of discharge diverted, based on averages of all discharge cross-sections taken following diversion, revealed that, on average, approximately 35% of low flow had been taken off from the Molenaars River, 80% from the Du Toits, and 82% from the Riviersonderend (Table 3.1). However, the higher instantaneous discharges (Q_{inst}) recorded at surveyed cross-sections were preferentially used in analyses (as per Figure 4.7). Care was taken to ensure that the flow of water into the offtake pipes was maximised and unobstructed, so that the percentage reductions in flow remained roughly consistent with natural upstream discharge fluctuations over time. This also reduced the risk of overtopping of the diversion weirs during occasional summer runoff events. Each flow reduction represented a disturbance potentially affecting in the order of 500 m^2 of riverbed; Resh *et al*. (1988) noted such larger-scale disturbances, though

more difficult to achieve and less replicable, might yield more persistent effects than small-patch bed disturbances.

Independent, concomitant (as far as possible), temporal replication was achieved by sampling both locations at each site twice before flow diversions were operational, twice during the flow reduction phase, and twice after the diversions were removed and natural flow regimes were reinstated. Table 3.1 indicates the durations, and start and end dates of each experimental flow phase (see Appendix 3.1 for individual sampling dates). The temporal sequence of sampling was dependent both on the expected time scale of invertebrate response (based on a review of literature) and on natural flow ranges over the summer period, but was limited to six occasions by pragmatic considerations, such as the time required to collect the requisite number of samples from each site (Underwood 1993). The duration of the total flow reduction phase of the experiment therefore depended to some extent on the time required to sample each of the locations at each site, for both the February and March trips. Sampling was staggered as best as possible, to enable fairly similar durations between sampling events at each location and site, for comparative purposes.

The study encompassed an entire dry season, extending from 3 December 1994 to 17 May 1995, a total duration of 166 days (Table 3.1). The dry season in the southwestern Cape is typically represented by the months of Nov-Mar, with the months either side, constituting spring and autumn transitional periods. Although the experiment should have spanned the months of October-March, permission for the experiment from DWAF and a test of field procedures on the Zachariashoek River (unpubl. data) delayed the onset of the fieldwork until December. Fortuitously, late rains resulted in higher than average flows during Oct-Nov 1994, and lower than average rains were experienced at all sites during the dry season. Additionally, flow increases signalling the onset of autumn occurred late in May, so the study was completed before commencement of the first major winter rains. Specific dates for field trips, and the numbers of samples and data sets collected in each instance, are provided in Appendix 3.1. All except one of the six sampling trips conducted from December to May was completed within a single month. For the third trip, all sampling for the Du Toits and Riviersonderend sites, and invertebrate collections for the other two sites were completed in February, but physical habitat surveys for the Molenaars and Elands sites extended into early March, due to DWAF logistical delays.

3.2 METHODS FOR SITE HYDROLOGICAL CHARACTERIZATION, WITH SPECIFIC REFERENCE TO LOW FLOWS

3.2.1 Collation of historical flow records and assessment of data quality

Table 3.2 summarizes the availability and quality of the observed historical daily flow records from DWAF hydrological gauging stations at the four sites, which were analysed for this study (see also Table 2.2). Observed data were screened for errors, missing data and periods of weir overtopping (exceedences).

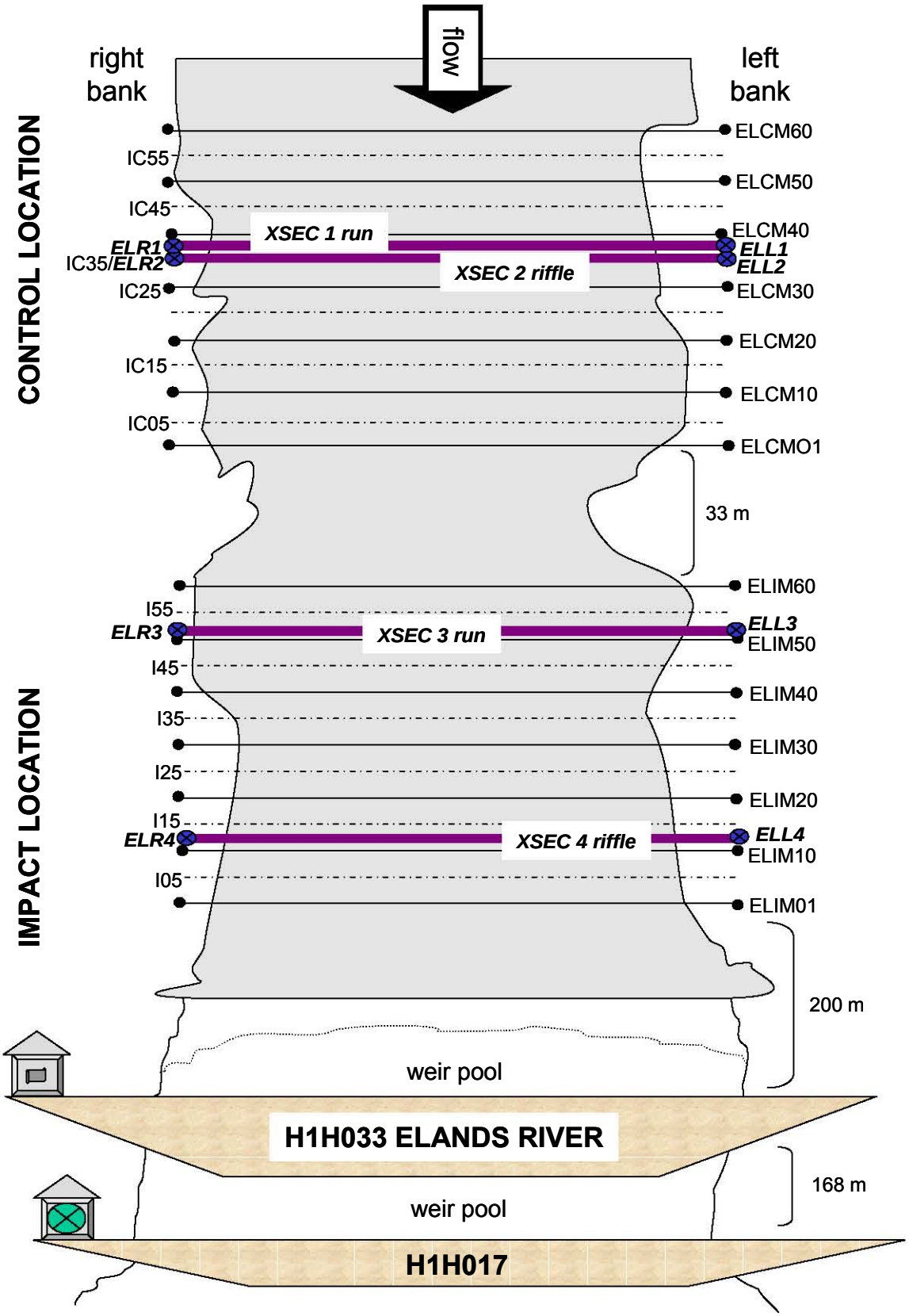


Figure 3.2 **Schematic of the Elands (EL) site, showing the 60 m control and impact locations.** As the control site, it had no diversion weir. Positions of transects delimiting each location and four cross-sections (XSEC1-4) are indicated. Gauging weirs H1H033 and H1H017 (non-operational) are shown. See Appendix 3.3 for explanations of survey codes.

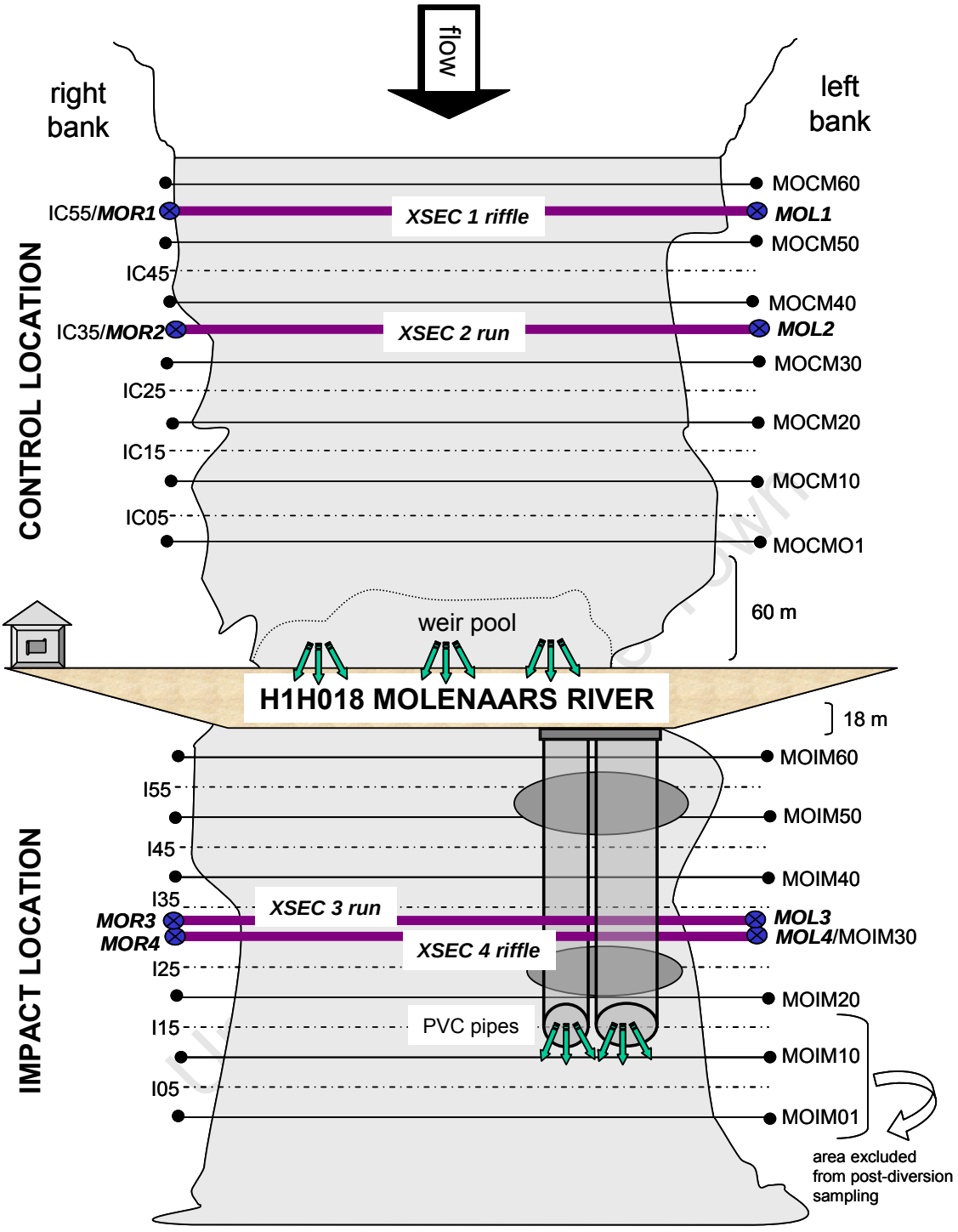


Figure 3.3 **Schematic of the Molenaars (MO) site, showing the 60 m control and impact locations.** Diversion of about 35% of natural low flow took place at existing gauging weir, H1H018, with water reintroduced to the site at the downstream end of the impact location. Shaded ellipses represent boulders used as props for the two offtake pipes. Positions of transects delimiting each location and four cross-sections (XSEC1-4) are indicated. See Appendix 3.3 for explanations of survey codes.

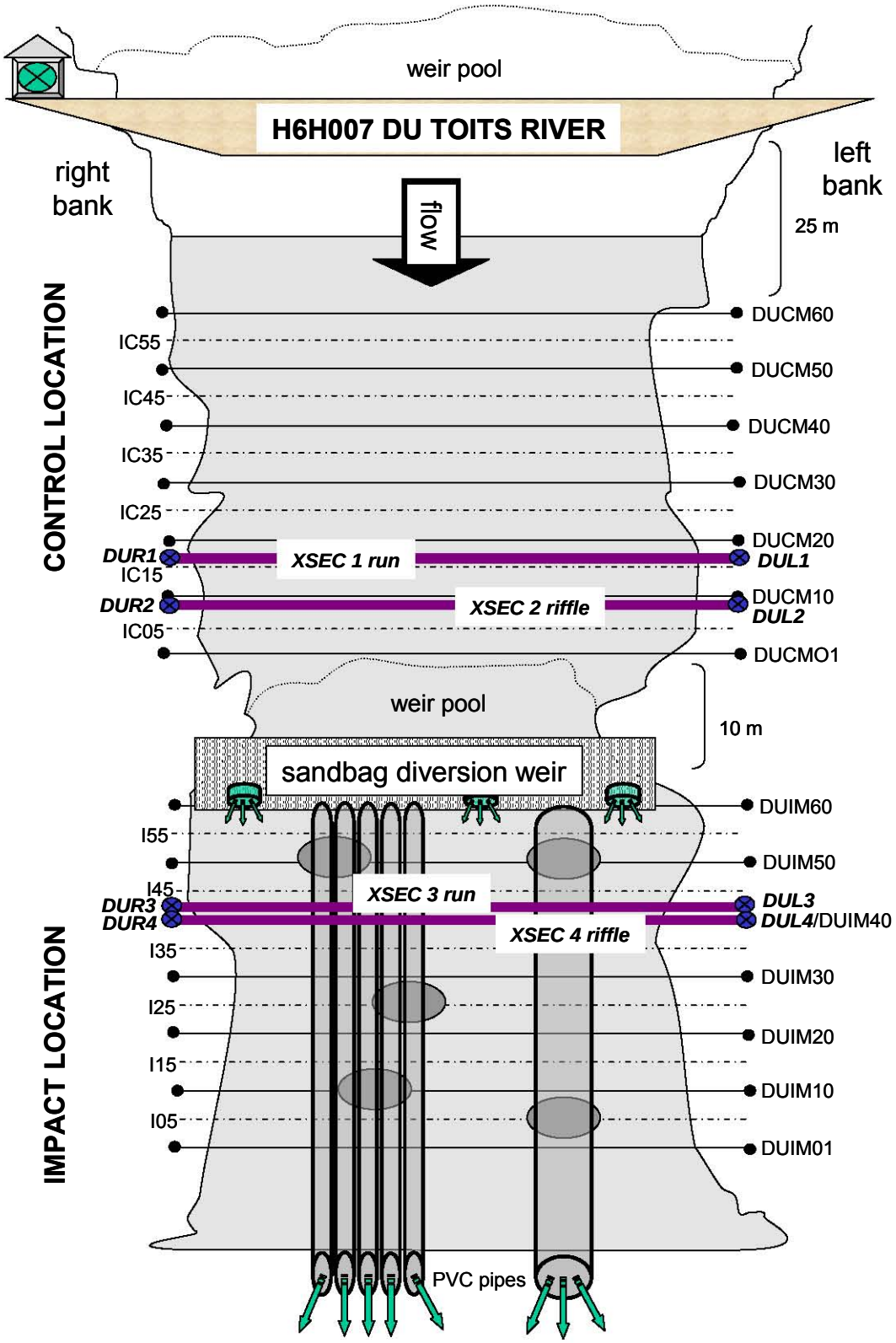


Figure 3.4 **Schematic of the Du Toits (DU) site, showing the 60 m control and impact locations.** About 80% of natural low flow was diverted at a weir above the impact location and reintroduced below it. Shaded ellipses represent boulders used as props for two sets of offtake pipes. Positions of transects delimiting each location, and four cross-sections (XSEC1-4) are indicated. Gauging weir H6H007 (non-operational) is shown. See Appendix 3.3 for explanations of survey codes.

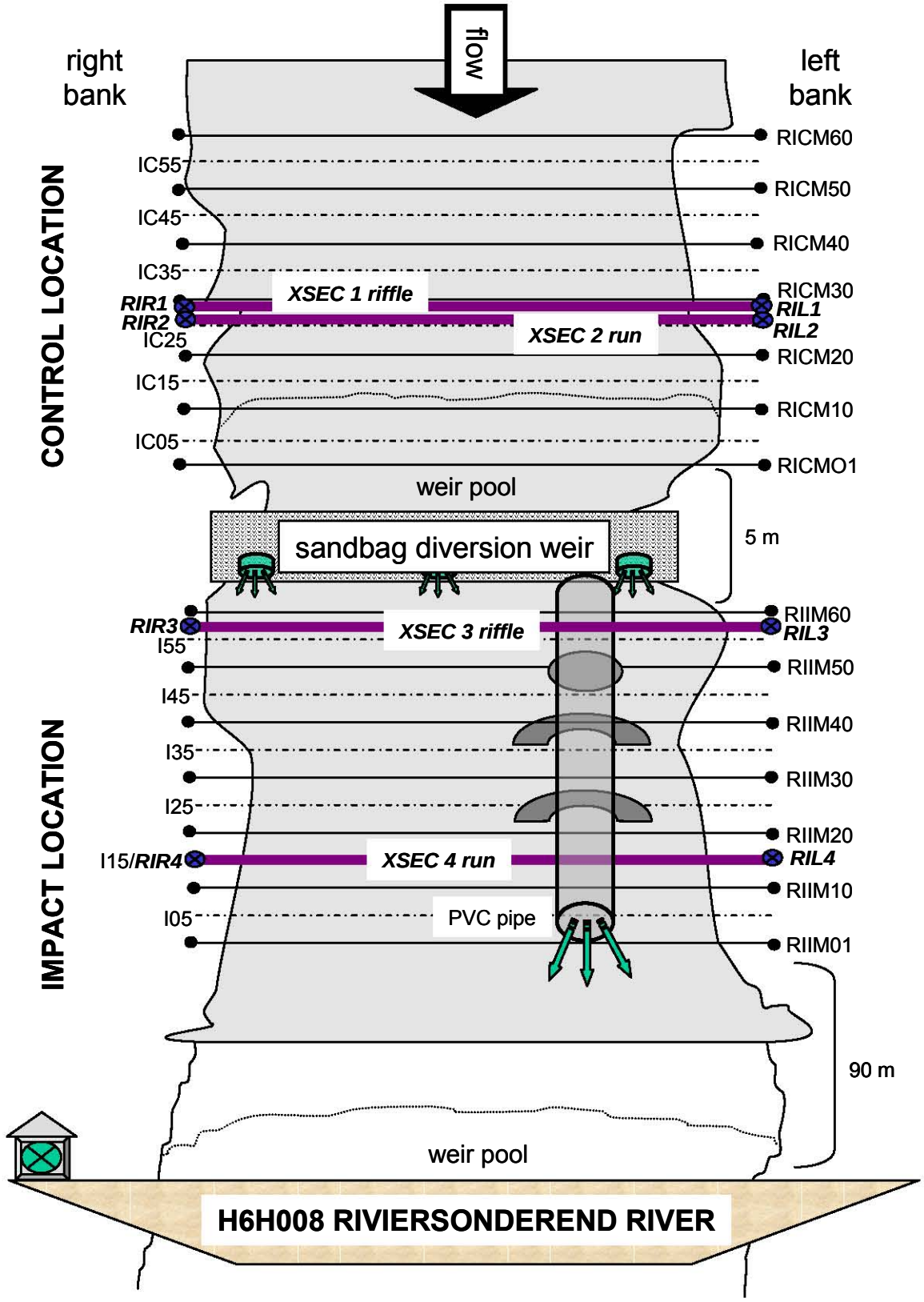


Figure 3.5 **Schematic of the Riviersonderend (RI) site, showing the 60 m control and impact locations.** At least 82% of natural low flow was diverted at a weir just upstream of the impact location and reintroduced to the site below it. Shaded ellipses and semi-circles represent boulders and wooden props for the single offtake pipe. Positions of transects delimiting each location and four cross-sections (XSEC1-4) are indicated. Gauging weir H6H008 (non-operational) is shown.

Table 3.1 **Timing and duration of pre-impact, impact and post-impact phases of the low flow study.** Durations were calculated on the basis of first and last sampling dates for the pre- and post-impact phases for the three experimental sites and for all phases for the control site (Elands). For the impact phase, at the experimental sites, durations were based additionally on the dates of completion and dismantling of the temporary flow diversion weirs. *Reduction percentages are approximate averages, while instantaneous discharge figures were used in analyses.

SITE	PRE-IMPACT PHASE		IMPACT PHASE			POST-IMPACT PHASE	
	TIMING	DURATION (days)	TIMING	DURATION (days)	DISCHARGE REDUCTION (%)	TIMING	DURATION (days)
ELANDS							
Control location	14/12/94-18/02/95	67	19/02/95-09/04/95	50	0	10/04/95-17/05/95	38
Impact location	13/12/94-26/02/95	76	27/02/95-19/04/95	52	0 (control)	20/04/95-17/05/95	28
MOLENAARS							
Control location	18/12/94-16/02/95	61	17/02/95-10/04/95	53	0	11/04/95-16/05/95	36
Impact location	18/12/94-19/02/95	64	20/02/95-03/04/95	43	*35	04/04/95-16/05/95	43
DU TOITS							
Control location	05/12/94-14/02/95	72	15/02/95-08/04/95	53	0	09/04/95-12/05/95	34
Impact location	05/12/94-14/02/95	72	15/02/95-03/04/95	48	*80	04/04/95-12/05/95	39
RIVIERSONDEREND							
Control location	03/12/94-10/02/95	70	11/02/95-07/04/95	56	0	08/04/95-11/05/95	34
Impact location	03/12/94-09/02/95	69	10/02/95-03/04/95	53	*82	04/04/95-11/05/95	38

None of the rivers were highly regulated upstream of the sites, so the historical flow records represent near-natural flow conditions (verified prior to the pilot survey using non-homogeneity tests; Joubert and Hurly 1994). Determination by Ninham Shand Consulting Engineers Inc. (NSI) of mean annual runoff (MAR) figures for the sites from observed data included estimates of water use by alien vegetation (for 1969-1993) upstream of the Molenaars and Du Toits sites, at 0.64 Mm^3 and 0.37 Mm^3, respectively (DWAF 1997). However, in both cases, naturalised and current MAR figures could be considered highly similar (Table 2.3). In the case of the Elands and Riviersonderend sites, present-day MAR could be assumed equivalent to naturalised MAR, as there were no major changes in land cover or use in the catchments upstream (DWAF 1997; Table 2.3).

Table 3.2 Availability and quality of site hydrological data (average daily discharges).

SITE	DWAF GAUGING WEIR(S)	START AND END DATES OF RECORD USED	NO. OF YEARS OF RECORD	NO. OF DAYS OF MISSING DATA	NO. OF DAYS OF WEIR EXCEEDENCES
Elands	H1H017 and H1H033	11/03/1969 - 26/02/1997	29	321	11
Molenaars	H1H018	27/02/1969 - 31/01/1997	29	249 (includes 43 days during experimental impact phase)	8
Du Toits	H6H007	01/10/1964 - 31/08/1992	29	353	536
Riviersonderend	H6H008	01/10/1964 - 30/06/1992	29	208	349

Twenty-nine years of hydrological data were available for use in hydrological analyses for all sites, excluding the total numbers of missing days (Table 3.2). The record length was considered adequate to reflect the dynamic character of the flow regime for the purposes of this study (e.g. Beran and Gustard 1977; Hughes 1987; Section 1.2). Although some periods of low accuracy data were used in the analyses, for all sites the potential for error was concentrated in the high flow component of the hydrograph and low flow data were sufficiently reliable; Table 2.2 presents weir accuracy estimates for all sites. For the Elands site, discharge records for weir H1H017 were used only until the day for which the first record was available for the new weir, H1H033, located just upstream; data from H1H033, which commenced recording in 1991, were used for the entire period of record overlap. At the Molenaars site, as the historical record included the period 20/02/95-03/04/95 for which flows has been experimentally reduced at the site (Section 3.1), discharges for these 43 days were excised from the record prior to analyses (Table 3.1). As weir H6H007 at the Du Toits site was closed in 1992, there were no discharge figures for the duration of the low flow experiment. Similarly, gauging weir, H6H008, at the Riviersonderend site was closed in 1992. Subsequent to many of the hydrological analyses performed for this study (Chapter 4), DWAF revised the observed data for the Du Toits and Riviersonderend sites upwards to account for measurement inaccuracies associated with

weir overtopping, primarily affecting flood estimates. The implications of the revisions are discussed in Chapter 4, where they were of relevance to the results.

3.2.3 Methods of analysis of historical flow records

Analysis of the natural hydrological regime may take many different forms, depending on the types of data and methods available, and information required, generating numerous general, low and high flow indices. The terms 'low-flow measure' and low-flow index' are often used interchangeably in the literature, as are 'flow variable' and 'flow statistic', and hence in this thesis as well (but see, e.g., Smakhtin and Watkins (1997) and Puckridge *et al*. (1998), who differentiate among them). Descriptions of standard and low-flow hydrological analyses, particularly, are provided in numerous sources (e.g. Beran and Gustard 1977; Nathan and McMahon 1990a; Gordon *et al.* 1992; Smakhtin (2000) provides a bibliography).

Where possible, the complete historical flow record for each site, and not only coincident periods of record, was used in analyses (Section 3.2.1). Records for days of weir overtopping were used, acknowledging that floods probably were underestimated. For several analyses, original observed data sets, inclusive of periods with gaps, were used, as indicated. Application of the Aquapack hydrological software (Gordon *et al.* 1992) for some analyses required entire daily flow data sets. Infilling of missing values was thus done, using the Hydrological Modelling Application System (HYMAS; Smakhtin and Watkins 1997). In the patching process, flow time series for gauging stations H1H018 and H1H017/33 were overlaid and compared. As the flow sequences were found to be similar, and as the sites were likely to experience similar rainfall-runoff patterns due to their proximity to each other, the two sites were patched from each other. Similarly, the daily flow data for the Du Toits and Riviersonderend rivers were patched from each other; flow records had been revised prior to patching.

Derivation of flow indices

Characterization of site hydrological regimes from streamflow time series was achieved using a suite of select, commonly applied flow variables that included recognised ecohydrological indices of low and high flows and flow variability (e.g. Q_{min}, Q_{95}, Colwell's predictability indices, CV). Flow variables represented three main groups similar to those adopted by Clausen and Biggs (2000) (Table 3.3):

1. *General flow variables*

   Attention also was placed on variables expressing the overall features of the hydrological regime and its variability. Within this group, select indices of low flow and high flow variability were included.

2. *Low flow variables*

   Greatest emphasis was placed on a large set of low flow measures, with specific attention to flow magnitude and, to a lesser extent, the timing and frequency of events. No direct attention was paid to measures of low flow duration or rate of change in flow, although seasonal elements were factored into the analysis (e.g. through the use of the 'Dry' subset of indices).

3. *High flow variables*

   Although unlike many other ecohydrological studies the emphasis of this study was on low flows, it was considered important to include select indices reflecting the relative influence of high flows.

The flow variables used in this study were ones that that could be generated using a range of readily available hydrological methods and programs, as described below. Depending on the objectives of the analyses, flow variables were determined at annual or monthly scales, and using flow data as average daily discharges or monthly flow volumes (e.g. Smakhtin *et al*. 1998). For most flow indices examined, the values derived were dependent on the temporal window examined, as well as the length of record used in each analysis (e.g. Beran and Gustard 1977). In several instances, various time series of flow indices were generated.

For calculating flow variables, DWAF records of average daily discharges were converted to NSI format, for analysis in Aquapak (Gordon *et al.* 1992), Microsoft Excel 2000, STATISTICA 6.1 (StatSoft 2001), or NSI programs Table and Series (unpubl. software, NSI, Cape Town). Summary data were automatically rounded to two decimal places by the NSI programs, although observed flow records were recorded to three places. In some instances, it was necessary to edit-in a third decimal place for very low flows (e.g. Du Toits site, January 1988, Q_{min} = 0.003 $m^3 s^{-1}$). Monthly flow data (as volumes, Mcm) were derived from the patched, daily time series of flows using the Aquapak program, SUMUP (Gordon *et al.* 1992).

Analysis of flow duration curves

Flow duration curves (FDCs) are widely used in hydrological studies to depict the relationship between the entire range of discharges (low to extremely high magnitude) and the percentage of time each of them is equalled or exceeded, over the duration of interest (Gordon *et al.* 1992; Smakhtin 2001). Importantly, although both flow magnitude and duration are accounted for, the actual sequence and timing of flow events are not considered. For instance, rivers with similar FDCs may differ markedly in the way the low flows days are distributed or grouped into short or long time spells. Moreover, probability functions cannot be fitted to the data, due to the serial correlation of flows, especially when the data are analysed over short durations (Gordon *et al.* 1992). Period of record and hydrometric errors are known to influence the shape and hence, interpretation of FDCs (Smakhtin 2001).

Historical average daily discharge records (non-patched) were used to develop a series of FDCs of natural flow for each of the sites. In all cases, the FDCs were constructed using these daily flow time series, enabling the depiction of variations in the flow data that tend to be smoothed out through averaging at monthly or annual scales (Gordon *et al.* 1992). Long-term, average annual FDCs (also known as period of record FDCs; Smakhtin 2001) were derived on the basis of the entire period of record. Additionally, long-term, average monthly FDCs were derived for specific months, using data from all similar calendar months from the whole period of record (e.g. January monthly FDC), a less common, but accepted approach (D. Hughes, IWR, Grahamstown, pers. comm.; Gordon *et al.* 1992; Smakhtin 2001). Curves were also

constructed for a low-flow window spanning the three, peak dry season months (Jan-Mar), in a similar approach to that of Petts *et al.* (1999). Flow duration curves were plotted untransformed, rather than as log-normal probability plots, using actual flow units.

To enable direct inter-site comparisons across the range of river hydrological regimes, in certain instances flow variables were standardized by the median annual or median monthly discharge (Q_{50}), an approach adopted in ecohydrological studies elsewhere (Jowett and Duncan 1990; Clausen and Biggs 1997, 2000), and were thus dimensionless; other common normalisation practices include division of discharge by catchment area, or expression of discharge as percentages or ratios of MAR or Mean Daily Flow (MDF) (Poff and Ward 1989; Gordon *et al.* 1992; Hughes 2001; Smakhtin 2001). The median flow was used, as it is less likely to be influenced by extreme events (and data collection errors) than the mean (Clausen and Biggs 1997; Bragg *et al*. 2005); streamflow time series tend to be positively skewed with the median flow often smaller than the MAR (Smakhtin 2001). The annual median had particular relevance for this study, as it has been proposed as the conservative upper bound for delimiting a river's low flow regime (McMahon and Finlayson (2003), with the area under the Q_{50} threshold approximating the total annual baseflow under natural conditions (Smakhtin 2001). It should be noted that the median is a guide, with percentiles of 75% and above not considered low flows in some studies. For instance, Padmore (1997) considered Q_{82} to be a moderate, not a low, discharge in flow-based analyses.

For each type of FDC, a range of standard flow percentiles (Table 3.2) was generated from a combination of the NSI Series program and the DRIFT hydrological software program, FDC (Brown and King 2002). The latter program also was used to calculate precise percentiles corresponding with Q_{inst}, Q_{min} and Q_{7dLow} figures. The BFI (Table 3.3) used as an index of baseflow contribution (Gordon *et al.* 1992; McMahon and Finlayson 2003), was calculated at annual and monthly temporal scales from the appropriate FDCs. Although Gordon *et al.* (1992) considered low-flow spell analysis of greater potential than FDC analysis for ecological purposes it has seldom been used for this purpose (but see Arthington *et al.* 2000) and was not applied here.

Indices of flow variability and predictability

The variability of the hydrological regime was described primarily using the coefficient of variation (CV; Zar 1984) for different temporal windows. The CV is an appropriate comparative measure of variability in that sample variance is adjusted by the mean, rendering the index dimensionless and insensitive to temporal variation (Hughes 1987; Poff and Ward 1989; Poff and Allan 1995; Palmer *et al*. 1997; Clausen and Biggs 2000). Since CV is generally small, it is often expressed as a percentage:

Table 3.3 Variables used in the hydrological characterization of the sites, with specific reference to low flows. Abbreviations used in this study and units are indicated. Q - discharge; FDC - flow duration curve; Mm^3 - million cubic metres or Mcm. *m* indicates a user-defined time period (e.g. *n*-days or *n*-months).

VARIABLE (abbreviations; units)	DESCRIPTION
General	
Mean annual runoff (MAR; Mm^3)	Mean of the total volume of annual runoff, over the period of record.
Mean annual flow (MAF; $m^3 s^{-1}$ x 1 year, or Mm^3)	Mean of the total annual discharge, over the period of record. As a volume, it is equivalent to the MAR.
Mean daily flow (MDF; $m^3 s^{-1}$)	Average daily discharge over the entire record.
Monthly flow volume (Mm^3)	Volume of flow recorded for each calendar month, as a total for each year of record or as an averaged total over the entire record.
Monthly mean daily average discharge (Q_{mean}; $m^3 s^{-1}$)	Mean discharge for each month of the year, for each individual year of record.
Monthly Mean Mean daily discharge (Q Mean Mean; $m^3 s^{-1}$)	For each calendar month, the mean of all average daily discharges recorded calculated over the entire flow record.
Monthly maximum daily average discharge (Q_{max}; $m^3 s^{-1}$)	Highest recorded discharge for each month of the year, for each individual year of record.
Monthly Max Max daily discharge (Q Max Max; $m^3 s^{-1}$)	For each calendar month, the maximum of all annual maxima, as average daily discharge, over the entire flow record.
Monthly Median daily average discharge (Q_{50}; $m^3 s^{-1}$)	Median discharge for each month of the year, for each individual year of record (i.e. the middle value in a ranked time series).
Monthly Modal daily average discharge (Q_{mode}; $m^3 s^{-1}$)	Modal discharge for each month of the year, for each individual year of record.
Instantaneous discharge (Q_{inst}; $m^3 s^{-1}$)	The actual discharge recorded at any instant in time.
Colwell's indices of predictability (P, C, M; 0-1)	Predictability of the hydrological regime (*P*), calculated as the sum of constancy (*C*) and contingency (*M*). Calculated on an annual basis (standard) and with a focus on the low flow regime (low flow).
Coefficient of variation (CV; 0-1 or %)	Variability of the hydrological regime, calculated on an annual, monthly or *m*-monthly basis.
Low flow	
Monthly minimum daily average discharge (Q_{min}; $m^3 s^{-1}$)	Lowest recorded discharge for each month of the year, for each individual year of record. Also calculated for the peak dry season.
Monthly Min Min daily discharge (Q Min Min; $m^3 s^{-1}$)	For each calendar month, the minimum average daily discharge over all years of record, calculated from the minima for each year of record. The lowest recorded discharge may be referred to as the Absolute Minimum Flow (AMF).
Monthly 7d-low flow (Q_{7dLow}; $m^3 s^{-1}$)	Average daily discharge over a period of seven consecutive days, and equal to the lowest of all discharges calculated for the various 7-day series within a month. The 6 days from any preceding month are used in a month when identifying the lowest flow series of 7 days.
Median 7-d low (Median Q_{7dLow}; $m^3 s^{-1}$)	Median value of all the 7-day low flows, over the entire record.
Percentage exceedence values or flow percentiles (Q_{75}, Q_{80}...Q_{99}; $m^3 s^{-1}$)	Proportion of time during which a discharge is equalled or exceeded. Calculated: on an annual basis over the whole period of record, independently for each calendar month, or for a three-month period representing the peak dry season (Dry). Average daily discharges correspond with the various percentage exceedence values derived from the annual, monthly or *n*-monthly FDC.
Index of baseflow contribution (BFI)	Baseflow index derived from the ratio of Q_{90} and Q_{50} (derived from FDC percentiles).
High flow	
Percentiles (Q_1, Q_5, Q_{10}, ...; $m^3 s^{-1}$)	Percentiles derived from FDCs in the same way as the low flow percentiles, but reflecting higher flows.
Index of variability (I_v or IV)	Characterization of the year-to-year variability of peak floods. Referred to as a 'flash flood index', as rivers with high I_v values are likely to exhibit flash flood behaviour.
Indices from flood frequency analysis (e.g. 1: 2, 1: 5, 1: 10 etc. ARI event)	Average return intervals (ARI) of flood events of different magnitudes.

$$CV = \frac{s}{\bar{x}}$$ **Equation 3.1**

Where:
s = standard deviation
$\bar{x}$ = mean

The index of variability (I_v) for higher flows and CV values were computed from patched daily flow records. The I_v index (see Gordon *et al.* 1992, p. 475, Equation A1.8) was calculated using the Aquapak program STATS. The higher the I_v value, the greater the inter-annual variability of peak floods. A further index of variability of daily flows, calculated from the slope of the annual or monthly FDCs, provided an estimate of the standard deviation of the logarithms of discharges ($S_{\log x}$) (Gordon *et al.* 1992; Brizga 2000), with higher values of $S_{\log x}$ indicating higher variability. $\text{Log}_{10}(x+1)$ was used to eliminate negative values. The index was calculated as follows, using the corresponding FDC data for each calendar month of the study and a standard coefficient:

$$S_{\log x} = \frac{\log Q_5 - \log Q_{95}}{3.29}$$ **Equation 3.2**

Colwell's indices are measures of predictability based on the mathematics of information theory, first proposed by Colwell (1974) to describe the general characteristics of periodic physical and biological phenomena. They are considered by some researchers (Stanford and Ward 1983; Gordon *et al.* 1992), to be particularly suited to comparisons of flow regime predictability among rivers, a critical feature in understanding whether or not a flow event constitutes a physical disturbance to the river (Sections 1.3 and 1.4), as they address the intensity and frequency of flows, as well as seasonal aspects of the annual hydrograph. The indices have been applied in a wide range of river ecohydrological studies, including by Resh *et al*. (1988), Bunn *et al.* (1986), Poff and Ward (1989), Rader and Ward (1989), Poff and Allan (1995), Poff (1996) and Clausen and Biggs (1997, 2000) (Section 4.1). Some authors have questioned the suitability of the indices for hydrological analyses (Walker *et al*. 1995; Poff 1996; Puckridge *et al*. 1998), so results for this study were treated with circumspection.

Predictability (P) is a measure of the variation among successive periods in the pattern of periodic phenomena (when variability is low, predictability is high; Colwell 1974) and of the relative certainty of knowing a state at a particular time (Gordon *et al.* 1992). It is calculated as the sum of two components, constancy (C) and contingency (M), where all indices range between 0 and a maximum of 1 (i.e. $P = C + M$; see Colwell (1974) for equations). Constancy is a measure of temporal invariance, with a value of 1 indicating that the same state is maintained across the entire period of interest, and it is always lower or equal to P for a given site (Clausen and Biggs 2000). Contingency describes the extent to which different states

correspond to different time periods, and is minimal (0) when the probability of occurrence of each state is independent of time period (i.e. it is an inverse measure of persistence). For example, a spring-fed stream may have a predictability close to one, most of which would be due to flow constancy (i.e. the proportion of C/P is high) (Poff and Ward 1989). In contrast, high predictability in a river with highly variable flow with a fixed periodicity would be mostly a function of contingency. Maximum predictability can be attained through complete constancy, complete contingency, or some combination.

The indices were calculated using the Colwell program in Aquapak (Gordon *et al.* 1992), which processes flow data at a monthly time step, using water years (starting month of October for Southern Hemisphere rivers; R. Nathan, Aquapak program developer, Sinclair Knight Merz, Australia, pers. comm.). A matrix was constructed of the states of the phenomenon of interest (rows) by time periods within some cycle (columns): for this study, months of the year by pre-assigned flow classes. Entries in the matrix represented the number of months in which the flow fell within the given interval, and the indices expressed the degree to which flow states were predictably distributed across months within the annual flow regime. A first analysis was undertaken adopting the seven default flow categories (Gan *et al.* 1991): $< 0.5\,\overline{Q}$, $0.5\,\overline{Q}$-$1.0\,\overline{Q}$, $1.0\,\overline{Q}$-$1.5\,\overline{Q}$, ..., $> 3\,\overline{Q}$, where $\overline{Q}$ = mean monthly discharge or volume; flow data were untransformed. Seven flow classes were also used by Clausen and Biggs (2000) across a wide range of river sizes. In a second analysis, indices were generated using 15 flow classes ($< 0.125\,\overline{Q}$ to $> 1.750\,\overline{Q}$) to focus on dry season flows.

The computation method is sensitive to both the length of the flow record and the typically inconsistent way in which the continuous streamflow data are divided into state classes (Gordon *et al.* 1992; Clausen and Biggs 2000). Gan *et al.* (1991) documented a bias towards high values of *P* and *M* for shorter lengths of hydrological record, with a recommended minimum record of 10-15 years (27 years were used here); indices were found to stabilise at 40 years and above. Moreover, they found that too few state classes could result in a bias towards high constancy, while too few categories could generate low predictability but high seasonality. In the present study, the method exhibited sensitivity to measurement units and, as expected, to analysis of water years versus calendar years. As the implications of subdivision into a higher number of low flow classes (and concomitant reduction in high flow classes) for the seasonal analysis remain unknown and largely untested elsewhere, the resultant indices served simply as a basis for relative comparison among sites.

Frequency analyses of low and high flows

Inter-annual flow extremes highlight the range of hydrological conditions to which biota have been exposed, even in river systems of relatively low variability (McMahon and Finlayson 2003). In low-flow frequency analysis, a low-flow frequency curve is produced showing the average interval in years (i.e. return period or recurrence interval) that flows in a river fall below a given discharge (or equivalently, the proportion of years

when a certain discharge is exceeded) (Gordon *et al.* 1992; Smakhtin 2001; Midgley *et al.* 1994). The curve usually is constructed based on a series of annual flow minima (the lowest 1-day or monthly discharge, or volume), with a single value extracted from every year of continuous historical record; seasonal low flow frequency analysis is also possible, where minimum flows are selected from the season of interest (e.g. summer or winter low flows). In the case of daily data, the flow minima series of several different averaging intervals may be examined, from 1-day through to 284-day minima. For this study, monthly 1-day and 7-day minima were calculated (Table 3.3), using NSI programs. The method also may be used to calculate indices not considered here, but used in several low flow studies, such as the 7Q10, representing the 7-day minimum discharge with a ten year average recurrence interval (ARI) (Section 4.1). Flood-frequency analysis similarly was used to calculate the average return periods of a range of inter-annual floods (Table 3.3), using NSI software.

Principal components analysis of flow variables

A PCA was applied to a set of 32 of some 55 original flow indices derived for the study, comprising the three groups above (Table 3.3), using STATISTICA Version 6.1 (for physicochemical data, the equivalent PRIMER PCA program was used; Sections 3.3 and 3.4). The approach was similar to that used by Clausen and Biggs (1997, 2000) and Poff *et al*. (2006a) to summarize patterns of variation in hydrological character. Most of these flow indices reflected annual or season time steps, while additional monthly flow indices were used to link flow disturbance to short-term biotic response.

Principal components analysis, the theory underpinning which is detailed in Clarke and Warwick (2001) and StatSoft (2001), produces a low-dimensional ordination space in which similar sites/samples are close together and dissimilar sites far apart. The PCA program utilises a matrix of p variables by n samples to ordinate a plot of Euclidean distances between samples in multidimensional environmental space. Clarke and Ainsworth (1993) observed that the use of Euclidean distance is most effective if the data are approximately multivariate-normally distributed (i.e. pairwise relationships are linear and the data are not markedly skewed on any of the variable axes); data were transformed first when necessary. Data then were normalised so that all PC axes had comparable (dimensionless) scales, rendering the PCA correlation-based. In the two (or more)-component loading plot generated, each flow variable was plotted as a function of its loadings for the first two principal components (PC1 and PC2), where the loadings reflected the correlation coefficients between the flow variables and each principal component. The quadrants of the plot in which each variable lies and the distance from the two central axes ($x = 0$; $y = 0$) indicate the relative strength and direction (positive or negative) of the relationship between the variable and PC1 or PC2, respectively. Thus, variables clustered close to one another demonstrate a high degree of correlation; as the plot is bilaterally symmetrical, variables at opposite or diagonal corners are closely related.

The degree of intercorrelation among the multiple flow measures generated was examined, to minimize redundancy (Townsend *et al*. 1997a; Clausen and Biggs 1997, 2000; Olden and Poff 2003), though a fairly

high number of variables remained after this process. For PCA to be most useful it is preferable to have far more observations than variables in the dataset. Paring down of the number of variables may be achieved by omission of all but one of a group of variables that are mutually highly correlated (r = 0.95; Clarke and Ainsworth 1993). Clarke and Warwick (2001) suggested a rough guideline for a percentage of variance explained by the PCA that adequately reflects the overall structure of the dataset, of 70-75% of the original variation. At lower percentages, decreasing reliance should be placed in the results.

3.2.4 Methods for calculation of instantaneous discharge

Flow proportions representing discharge reductions at diversion weirs

Prior to initiation of any sampling during the impact phase, at least two discharge cross-sections were established at suitable places upstream and downstream of the temporary diversion weirs at the Du Toits and Riviersonderend sites, immediately following their construction. Cross-sections were placed in channel sections where the most accurate discharge measurements could be obtained, given the low flows. The calculated discharges (Equations 3.3 and 3.4) were used to establish whether or not the weirs were diverting the approx. pre-determined proportions of flow for each site; Molenaars diversion estimates were taken from the gauging record. As a result of experimental error in discharge measurement at low flows, however, the resultant proportion of discharge diverted from the Du Toits impact location was actually more similar to that diverted from the Riviersonderend location (at about 86%), than the expected figure of 80% (Table 3.1).

Instantaneous discharge at riffle and run cross-sections

Instantaneous discharges representing river flow at a specific time of day (cf. average daily discharge) were calculated for each of the riffle and run cross-sections on each trip, a total of 96 sets of measurements (Appendix 3.1). Field measurements and calculations of total discharge for each cross-section were based on the 'partial section concept' (Bovee and Milhous 1978), where each partial section or hydraulic cell across a cross-section is defined by the distance between the vertical at each point measurement of depth and average velocity, extending a specified tape distance to the verticals on either side (Equations 3.3 and 3.4).

The discharge through each partial section (q_i) was calculated using the following equation:

$$q_i = a_i \times v_i = w_i \times d_i \times v_i \qquad \textbf{Equation 3.3}$$

Where:
q_i = the discharge through a cell
a_i = the area of the cell
v_i = mean column velocity (0.6d or 0.6V), measured at the vertical
d_i = mean depth of the cell, measured at the vertical
w_i = width of the cell = the sum of a specified distance to each of the two adjacent verticals.

Total discharge through the cross-section (Q) was then calculated as the sum of the partial (cell) discharges:

$$Q = \sum_{q_i}^{n} = \sum (\bar{v}_i \times w_i \times d_i) \qquad \textbf{Equation 3.4}$$

Instantaneous discharges at a site were usually measured within a few hours of one another, but might have differed slightly from corresponding average daily discharges. During the peak dry season, however, Q_{inst} tended to approximate average daily discharge. Day-to-day minor discharge fluctuations were recorded when they occurred between days at which the two locations were sampled at a site, or between cross-section survey and biological sampling dates.

From 11-34 cross-channel point measurements of depth and velocity were used to calculate discharge (Section 3.4). These were evenly spaced across the channel in most instances, but additional measurements were made where distinct changes in surface flow type were observed or where additional bed elements became exposed with progressive flow reduction. Attempts were made to ensure that, in most instances, no more than 10% and preferably no more than 5% of the total discharge was flowing through any partial section (United States Geological Survey - Bovee and Milhous 1978). However, it became increasingly difficult to adhere to this guideline with decreasing discharge.

Constraints with hydraulic measurements at low flows

The instantaneous discharges calculated over the six-month period revealed several difficulties with low flow measurement across all sites. These problems are discussed here, as they have implications for the hydrological results presented in Chapter 4, habitat assessments of Chapter 6, and for low-flow assessment in general. The variability in discharge measurements resulted in differences for a site in the ranking of months from lowest to highest discharge, according to which sets of data were examined. This clearly demonstrated that the experimental error of measurement at low flow often exceeded small-scale, natural changes in dry-season flow. To minimise such error, where instantaneous discharges were used in analyses only the discharges calculated from run cross-sections were used, rather than an average of riffle and run discharges, for the reasons discussed below. Although riffle discharge data were excluded from the assessment, any major discrepancies between discharges for cross-sections or locations were noted (Chapter 4).

Experience and empirical evidence from hydraulic measurement at low flows have shown that it is more difficult to obtain accurate measurements of depths and mean column velocities (and water surface elevations, WSEs) in riffles than in runs. The hydraulic characteristics of riffles are more complex than runs, particularly as the influence of bed element roughness typically increases with decreasing discharge and flow is more turbulent (Davis and Barmuta 1989; Gordon *et al.* 1992; Wadeson 1996; Jowett 1998; Robson *et al.* 1999). Analysis of the degree of variability in discharge measurements from riffles compared with those

from runs showed that estimates for runs were generally less variable. Riffles also tended to cause Q_{inst} overestimates, although the trend was not consistent (see also Padmore 1997). Moreover, particularly for riffles, discharge measurements became progressively less accurate as flow decreased. Results obtained for the Elands site are used as an example here; similar levels of experimental error were encountered at the other sites. As the Elands represented the control site, discharges at the control and impact locations, and for riffles and runs, should have been similar for each month. Overall, the standard deviation, SD, associated with the mean of instantaneous discharges calculated for this site for each month ranged between 0.054 $m^3 s^{-1}$ and 0.146 $m^3 s^{-1}$. For the averages of discharges measured for the control and impact locations for the six sampling trips, SD ranges of 0.001-0.138 $m^3 s^{-1}$ and 0.04-0.194 $m^3 s^{-1}$ were obtained, respectively. The range of variability was lower for averages of run discharge measurements throughout the study, than for averages of riffle data, at SDs of 0.028-0.066 $m^3 s^{-1}$ and 0.003-0.106 $m^3 s^{-1}$, respectively.

As discharge decreased during the dry season, both naturally and through experimental manipulation, large proportions of flow were flowing through relatively small partial sections of the channel. Most notably, for the riffle cross-section (cross-section 3) of the Riviersonderend site, during the impact phase of the experiment (Feb-Mar), at least 64% of the discharge passed through a partial section 0.50 m wide by 0.13 m deep, representing only 0.05% of overall wetted channel width. This resulted in extremely high (*c.* 100%) experimental error in measurement. Comparison of calculated discharges before and after the known flow reduction of *c.* 86% for both months showed that the run discharge for the impact phase reflected the amount of water diverted, but the riffle discharge was consistently an order of magnitude less precise (0.101 $m^3 s^{-1}$ cf. 0.017 $m^3 s^{-1}$).

With the naturally heterogeneous riverbeds, hydraulic profiles were observed to break down at extremely low flows and accurate hydraulic measurement was difficult. The typical velocity profile, where the mean value of velocity occurs at about 0.6 of the water depth from the water surface (Gordon *et al.* 1992), was distorted at shallow depths, resulting in increased inaccuracies in point velocities (and hence, in discharge). The extent of distortion and its impacts on other aspects of flow hydraulics (e.g. shear velocity and roughness Reynolds number - Section 3.4) would require comprehensive field and laboratory calibrated research (Carling 1992; Young 1992; Padmore 1997), but are recognised here as diminishing the accuracy of the results obtained for both discharge and habitat hydraulics (Section 3.4).

3.3 METHODS OF DATA COLLECTION AND ANALYSIS FOR WATER CHEMISTRY

3.3.1 Field data collection and laboratory methods

Water chemistry data (here including physical parameters, e.g. temperature) were collected in control and impact locations at each of the sites for each sampling trip (dates in Appendix 3.1), producing 48 complete data sets, each of 21 variables. At least monthly, instantaneous measurements were made of each variable, to

assess whether or not secondary chemical effects of flow reduction occurred. Limitations of this regime included: the absence of repeated sampling at short time intervals both during the flow reduction phase and immediately after the temporary weirs were removed, when any poor-quality water might have been flushed from the system (but see Section 5.2); and the potential for rapid fluctuations in water quality to go undetected. Both locations at a site were sampled at roughly the same time of day, with main channel samples consistently taken from runs. As the primary objective was to identify any major chemical responses to changes in flow, samples were collected from flowing sections of the main channel, even during the experimental impact phase (i.e. a 'best-case scenario'). Additional measurements for variables that could be directly recorded in the field were made in isolated, non-flowing areas of the channel (typically pools), as well as in major biotopes, at both locations per site, to identify any extremes in variable ranges during the impact and post-impact phases; such areas were not encountered during December-January.

Instantaneous temperature was measured on site using a Syland Simplair Model F5SP oxygen meter, accurate to ± 0.1 °C. Readings were cross-checked with measurements obtained using a standard mercury thermometer (accurate to ± 0.5 °C). Measurements were made in the three main biotopes (riffles, runs and pools), as well as in any isolated standing waters. Longer-term, diel ranges in temperature in each location were recorded using minimum/maximum thermometers. Water pH was measured, in both the main channel and isolated pools, with a Crison Portable 506 field pH meter, accurate to 0.01 units. Electrical conductivity was measured in the flowing main channel and in isolated pools, using a Crison Conductimeter Portable 523 field meter with built-in temperature compensation of 25 °C. The meter is accurate to 0.1 μS cm^{-1} (accuracy > ± 0.3%; reproducibility > 0.2%). Conductivity values were recorded as μS cm^{-1} and converted to mS m^{-1}. Instantaneous measures of dissolved oxygen (DO) were obtained in the main flowing-water biotopes, as well as in isolated pools, using a portable Syland Simplair Model F5SP oxygen meter with inbuilt altitude compensation. An estimated of turbidity was obtained by visual inspection; the river bottom was visible at all sites over the study period.

Water for laboratory analyses of nutrients, cations and anions was sieved through an 80 μm-mesh and then filtered through pre-combusted and pre-weighed Whatman GF/F glass microfibre filters (pore size = 0.45 μm). A measured volume of approximately one litre of water was similarly filtered for laboratory analysis of total dissolved solids (TDS), and the filter paper was used for analysis of total suspended solids (TSS). All filtered water, except that for ammonium analysis, was bottled in polythene containers that had been pre-cleaned in 5% phosphate-free ExtranR solution, and rinsed in deionised and then double-distilled water. Samples for analysis of ammonium were stored in HCℓ washed glass vials, within polythene containers. All water samples were kept frozen while in the field, and in the laboratory until the time of analysis. Analyses took place within a maximum of one month from field collection date, to minimise storage contamination.

Concentrations of the anions $SO4^{2-}$, $C\ell^{-}$, and F^{-} were measured using a high-performance Dionex Ion Chromatograph (Haddad and Jackson 1990). Detection was by conductivity with chemical eluent

suppression. The anions were separated on an HPIC-AS4A anion exchange separator column, with a carbonate/bicarbonate buffer eluent. Calibrations were based on peak height, and results expressed in ppm (mg ℓ^{-1}), with an estimated accuracy exceeding 0.005 ppm. Results were then converted to mmol ℓ^{-1}. Levels of F^- were mostly below detection limits and were, therefore, excluded from further analyses. Concentrations of K^+, Na^+, Ca^{2+} and Mg^{2+}, as well as ammonium (NH_4-N), were measured using an HPIC-AS4A cation exchange separator column and the appropriate eluent. For both anion and cation analysis, the percentage error on repeat runs with the same standard was estimated at approximately 10%, and possibly greater for very low concentrations (< 0.5 ppm). Ammonium values were below the detection limit of 0.2 ppm (0.2 mg ℓ^{-1}) in all instances. A cation-anion balance method (Day 1990) was used to check that the sum total concentrations of anions matched those of cations. In three instances, total anion versus cation differences exceeded 0.1 mmol ℓ^{-1}, so reruns of the samples and three controls were done and the balance method successfully reapplied. Correspondence between major ions and TDS was confirmed, using the method recommended in Day (1990). Nitrates (NO^-_3-N), nitrites (NO^-_2-N), and phosphates (PO^{3-}_4-P), as well as reactive silicon (SiO_2-Si), were analysed using a TECHNICON AutoAnalyser II, with a detection limit of 1 μg ℓ^{-1} (Mostert 1983; Windt 1993). Results were expressed as either mg ℓ^{-1} or mmol ℓ^{-1} of the nutrient atom (i.e. NO^-_3-N, NO^-_2-N and PO^{3-}_4-P), and subsequently converted to μmol ℓ^{-1}. Total alkalinity (TA) was measured by titration of samples with 0.005 M ℓ^{-1} HCl (methyl orange indicator), according to the method prescribed by Golterman *et al*. (1978). Standardisation was against NaOH, titrated with 0.005 M ℓ^{-1} oxalic acid (phenolphthalein indicator). Three replicate titrations were performed for each water sample. The precision of the method was estimated at 2% at TA = 1 mmol ℓ^{-1}, and 2-10% at TA = 1-0.1 mmol ℓ^{-1}. Results were obtained as mg ℓ^{-1} $CaCO_3$, HCO^-_3 (bicarbonate), and expressed as mEq ℓ^{-1}. Carbonate alkalinity was not encountered.

Total suspended solids (TSS, mg ℓ^{-1}) were measured by filtering a known volume of water through GF/F filters of known pre-filtration dry mass in the field, drying the filters at 60 °C for 48 h, and then reweighing them (to 0.1 mg accuracy) to calculate the difference in dry mass; a correction factor was applied to account for minor losses in mass due to field handling. The organic fraction of TSS was calculated as a percentage for the sample filters, using the difference in mass before and after combustion of the dried filter at 450 °C for 4 h. Unfortunately, a fire resulted in the loss of most TSS filter papers. The TSS data from the pilot study (Chapter 2) and a subset of filters from the field experiment indicated however, that values tended to be negligibly low irrespective of site, location, month or treatment. An assessment was made of what proportion of the epilithon of individual stones, from which invertebrates were collected in each biotope, was organic, using the same method (Section 3.5). Calculation of total dissolved solids (TDS, mg ℓ^{-1}) was performed by evaporation at 60 °C of a known volume of pre-filtered water from pre-weighed lightweight glass beakers, reweighing post-evaporation (to 1 mg accuracy), with the difference in mass representing TDS concentration.

3.3.2 Methods of data analysis

To explore spatial and temporal trends in the chemistry data, time series were plotted for all variables, according to the actual days on which the data were collected. The three study phases were delimited on the basis of the dates of experimental diversion of flow and reinstatement of natural flow for the impacted location (Table 3.1). For the variables where data were collected both in a flowing section of the mainstream and in isolated, standing pools, error bars denoting upper and/or lower limits were included where the difference between the two measured values was greater or equal to an arbitrarily designated 10%. The extent to which an assessment of the potential impacts of abnormally reduced flows on the sites could be made was constrained by the relatively low number of observations per site. However, differences in water chemistry between location pairs for individual site, over the entire six-month period, were examined. It was hypothesised that significant differences in any chemical variables between locations for experimental sites might signal a pronounced effect of unnatural flow reduction. In contrast, significant between-location differences for the control site would indicate variables exhibiting naturally high spatiotemporal variability. The non-parametric Mann-Whitney U test was applied (STATISTICA 6.1), due to small sample sizes and occasional unequal sample variances. The former limitation was also overcome by *a priori* use of two-sided exact *P* values to designate degree of significance, accepting a small potential error as a result of any tied ranks (StatSoft 2001). Among-site similarities in chemistry over the study period were assessed by one-way, fixed effects ANOVAs for individual variables. Sample sizes (n = 48, with location data sets pooled) meant that test assumptions of normality and homoscedascity were met in most instances (Zar 1984). However, NO^{-}_{3}-N, inorganic-N and SiO_2-Si showed significantly non-normal distributions, on the basis of Kolmogorov-Smirnov (d) goodness of fit tests, and were $\log_{10}$ (x+1)-transformed. Tukey honestly significantly different (HSD) tests were used in cases of significant inter-site differences, to identify the site(s) responsible and their appropriate groupings.

Summary statistics were computed for each site and chemical variable, to show the observed natural ranges and variability (CV - Equation 3.1) in chemical conditions over the full dry season; as temperature data are on an interval not ratio scale, CVs are inappropriate (Zar 1984). For the flow reduction phase, direct comparisons were made, for each site and variable, between chemical concentrations at natural, peak low flows and values where flows were abnormally low. For the control site, the percentage difference between concentrations for each variable for the two locations provided an indication of the degree of natural spatiotemporal variability inherent in each constituent at peak low flows. A combination of a difference in control and impact concentrations that exceeded 30% at peak low flow (based on observed ranges in natural variability) and natural CVs, were used as indicators of a distinct difference in the magnitude change of a variable.

To gain insight into natural trends in water chemistry with natural and unnatural discharge decreases, and to identify potential key variables from a low flow perspective, discharge-concentration (Q-C) relationships were established. General trends were sought, so as to be able ideally to categorise chemical variables into

groups with distinct responses to low flows. Data for each chemical variable were therefore pooled, as far as possible on the basis of the ANOVA results for intra-site differences. In a few instances, the results of the Tukey multiple comparison test were inconclusive in terms of the subgroups to which sites were assigned, possibly as a result of inadequate statistical power due to small sample sizes (Zar 1984). In such cases where a site(s) straddled subgroups, Q-C relationships were determined for each subgroup, both inclusive and exclusive of the corresponding data for the particular site. It also was necessary to standardise flow conditions across sites, to account for relative differences in river sizes and the instantaneous nature of discharge. Normalisation was achieved by dividing the instantaneous discharge measured at each site by the corresponding monthly Q_{50}; relationships derived using Q_{inst} yielded similar or weaker results. The approach suggested by Malan and Day (2002a) for situations where only a simple, preliminary guide to the nature of Q-C relationships is required, was followed. Reliance in the strength of each Q-C relationship was placed on visual examination of trends in the data, in conjunction with calculated R^2 (coefficient of determination) values. The best least squares fit of a linear ($y = m\,x + b$), logarithmic ($y = c \ln x + b$), exponential ($y = c\,e^{bx}$) or power ($y = c\,x^b$) function was calculated, using Excel 2000; where all equations showed similar R^2 values, a linear or logarithmic relationship was selected as the simplest approach. For all except linear trend lines, a transformed regression model was used. Strength of the Q-C relationships was assigned to one of three categories (after Malan and Day (2002a) in similar research at regional scale): $R^2 > 0.5$ = strong correlation; $0.2 < R^2 < 0.5$ = moderate correlation; $R^2 < 0.2$ = weak correlation. The typically poor correlations obtained (Chapter 5) required that R^2 values below 0.05 be arbitrarily designated 'slight to non-apparent' and indicative of no relationship. Although $R^2 > 0.5$ represented a 'strong correlation', it was acknowledged that R^2 values above 0.75 would better reflect such a relationship, especially as the significance of R depends in part on n (Malan and Day 2002a; J. Day, FRU, UCT, pers. comm.). Although equations were fitted only for Q-C relationships for the main data set (channel flowing waters), data points representing chemical conditions in isolated control and location pools were included in graphical plots, for the corresponding mainstream discharges, to assess whether or not they supported mainstream trends.

The PRIMER Version 5.2.2 program, PCA, was used for exploratory multivariate ordination analyses of chemical (and physical habitat; Section 3.4) data sets among sites and low flow conditions during the study period, as well as for the pilot study (Chapter 2) (Section 3.2 provides a general method description). Essentially, PCA (Section 3.2) is more appropriate for ordination of environmental data than for community data, as: (1) there are no large blocks of zero counts; (2) there is a large, mixed range of measurement scales; and (3) some form of Euclidean distance is ecologically sound for this type of data. A deficiency of PCA in this context, however, is its poor preservation of distance, especially in the 2-d ordination plane (Clarke and Warwick 2001).

Draftsman plots for all combinations of chemical variables were used in conjunction with the Kolmogorov-Smirnov (d) goodness of fit test for normality (STATISTICA 6.1), recommended by Zar (1984) in the case of continuous distributions, to check for divergences from normality; transformations were performed where

required. A cation ratio (Equation 3.5) and an anion ratio (Equation 3.6), recommended in Day (1993) and Dallas *et al.* (1998), were used to reduce the dimensionality of the data set for PCA.

$$\frac{[Na^+]+[K^+]}{[Na^+]+[K^+]+[Ca^{2+}]+[Mg^{2+}]} \qquad \textbf{Equation 3.5}$$

$$\frac{[C\ell^-]}{[C\ell^-]+[HCO_3^-]} \qquad \textbf{Equation 3.6}$$

The anion, SO_4^{2-}, was retained independently for both main study and pilot analyses (Chapters 2 and 5, respectively). No variable pairs showed significant inter-correlations exceeding 0.95. However, oxygen values in riffles and runs were omitted from the PCA in favour of pool O_2 levels, as the former two measures tended to be similarly high in most cases, and correlated with each other at $r = 0.57$ ($P < 0.05$). High, significant ($P < 0.05$) inter-correlations between maximum, minimum and instantaneous temperature resulted in maximum temperature being selected as the best overall measure ($r = 0.78$-0.84, $P < 0.05$). Although a significant, high positive correlation was found between NO^-_2-N and NO^-_3-N (grouped as inorganic-N) and PO^{3-}_4-P ($r = 0.84$, $P < 0.05$), both variables showed sufficient differences across locations and flow conditions (Section 2.3) to warrant inclusion in ordination analysis. In the case of the strong negative correlation between $C\ell^-$ and inorganic-N ($r = -0.91$, $P < 0.05$), the former variable was incorporated in the anion ratio (Equation 3.6). The poor correlation between conductivity and TDS ($r = 0.41$, $P < 0.05$), considered a result of high experimental error due to pure waters at all sites, led to the latter variable being excluded. Ten variables were retained in the final PCA data set (Chapter 5).

Complete historical chemistry records available from DWAF for each site (Table 3.4) were downloaded, for comparison with the 14 variables measured at each site during the field study. The number of sampling records in any particular month was variable, and there were missing data for one or more chemical variables for any one sampling date. All records of zero concentration for a variable were edited out of the data set, as it was not specified in the database as to whether or not the zeros represented missing data or values below detection limits. The sets of records for the two sampling stations for the Elands site, corresponding with DWAF gauging weirs (Table 3.4), were merged for analyses.

Historical summary statistics were calculated for each site and chemical variable for: (1) all data falling within the months represented by the current study; and (2) only the months February and March, representing the peak low flow period corresponding with the impact phase. This approach enabled comparison of short-term chemical conditions with long-term patterns in water chemistry.

Table 3.4 Synopsis of available historical data on water chemistry at the sites, collected near the DWAF hydrological gauging stations.

SITE	DWAF SAMPLING STATION CODE(S)	START AND END OF DATA RECORD	TOTAL NO. OF RECORDS
Elands	H1H017Q01 H1H033Q01	Jun 1970 - Aug 1992 Jun 1995 - Aug 1999	747
Molenaars	H1H018Q01	Jun 1970 - Sep 1999	1019
Du Toits	H6H007Q01	Apr 1973 - Aug 1992	375
Riviersonderend	H6H008Q01	Feb 1967 - Aug 1992	378

3.4 METHODS OF COLLECTION AND ANALYSIS OF DATA ON INSTREAM PHYSICAL HABITAT

3.4.1 Field procedures for data collection for analyses of temporal and flow-related changes in physical habitat

General survey and biotope mapping procedures

To facilitate consistent collection of biophysical data within the study reaches, a 60 m reach was delineated for each location at each site using 100 m survey tapes and subdivided on the basis of transects, to produce the templates illustrated in Figures 3.2-3.5. For each location, transects were identified at 5 and 10 m intervals, numbered in an upstream direction, and secured above approximate bankfull water level (see Appendix 3.2, for survey codes depicted in Figures 3.2-3.5).

During the first habitat survey (Dec 1994), maps were produced for the control and impact locations at each site, using parallel survey-based and finer-detail freehand mapping to demarcate the extent of the wetted channel, major in-channel features (e.g. bedrock outcrops), and the approximate "boundaries" of individual biotope patches (see below for biotope identification method). On subsequent mapping trips (Jan-May 1995), changes in the distributions and surface areas of biotope patches were mapped entirely freehand, using the map from the previous visit as a baseline for identifying any flow-related change (DWAF biotope map data proved unusable). Surveying was performed using circular type prisms (accuracy 5 mm and zero correction 3 mm), mounted on a ranging rod, with one of three surveying instruments on different occasions: a Leica TC2002K Total Station (accuracy of 0.5 s, 1 ppm; i.e. accurate to 1 mm for every 1 km); a Nikon DT10ALG (accuracy of 3 s, 3 and 5 ppm; i.e. accurate to 3 mm for every 5 km); and a Pentax PSC (accuracy of 10 s, 5 and 7 ppm). Communication during surveying was by two-way radios, and data were recorded digitally, using a Psion Electronic Organiser II Model LZ and the Organisurv program.

For each location, the left and right waters' edges (WEs) of the channel (defined in a downstream direction) were surveyed at 5 m intervals. Additionally, at every 10 m transect, three WSEs were measured at intervals

across the wetted channel. Water surface elevations were typically evenly spaced, and taken at points where flow was least turbulent, to maximise accuracy. Where distinct changes in bed elevation or hydraulics were apparent across the channel, however, WSEs were spaced to reflect corresponding differences in the water surface. The spatial extent of large bed elements were surveyed, while spot shots were taken at the centres of smaller boulders, the dimensions of which were then measured with a survey tape (Appendix 3.2 provides survey codes used to represent habitat features). The following survey data were routinely recorded: site and location name; date; an automatically generated number for each spot shot and/or a specific code for a beacon (Appendix 3.2); the biotope code assigned to each spot shot (Appendix 3.2); X and Y (in combination representing horizontal distance) and Z (elevation) co-ordinates from a common datum, for each surveyed point. Site location maps were linked by survey benchmarks, used on all subsequent trips as points of reference; survey co-ordinates represented arbitrary datums not linked to national grid elevations.

Forty-eight biotope maps were generated for the sites (see Sections 3.4.2 and 3.4.3); trip dates are given in Appendix 3.1. An example is provided in Figure 3.6.

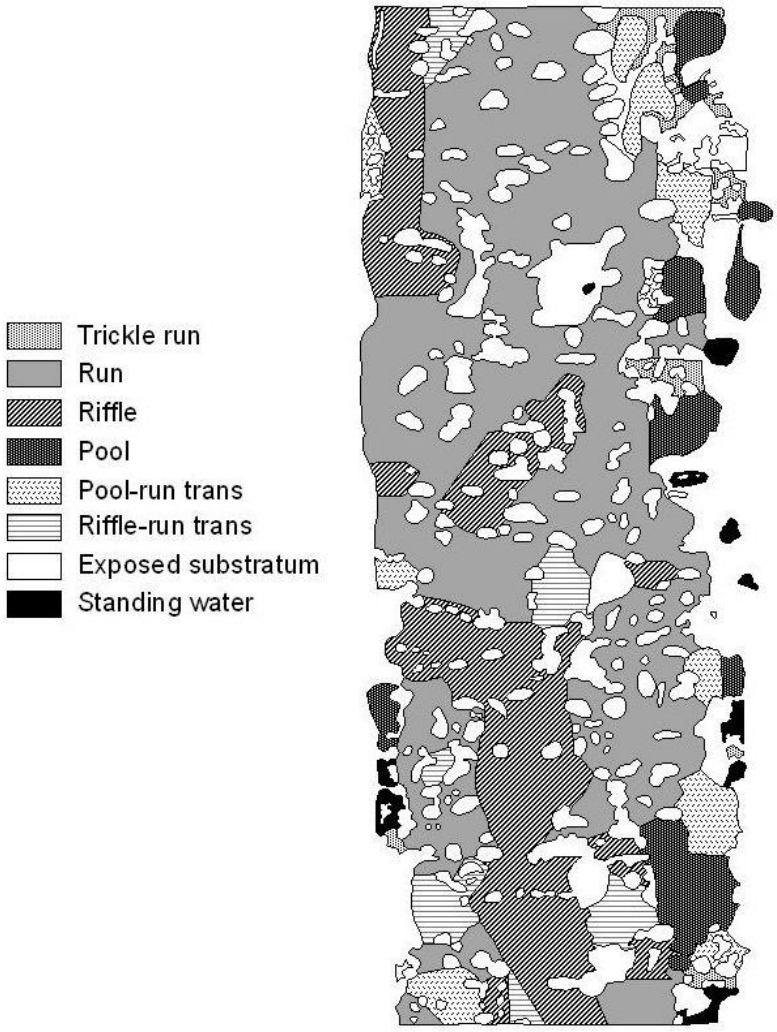


Figure 3.6 Biotope map for the impact location at the Molenaars site, December 1994.

Field identification of hydraulic biotopes

Of the range of established, ecologically meaningful habitat units for invertebrate assemblages, the hydraulic (physical) biotope was adopted for this study (Section 1.4.8 provides definitions). Hydraulic biotopes are recognized as relatively small (i.e. in the order of square metres) habitat patches spatially, with a characteristic range of temporarily variable hydraulic characteristics resulting from the interaction between flow, substratum and channel morphology. They are associated with larger scale, more persistent 'morphological units' (Wadeson and Rowntree 1998; King and Schael 2001) which occur at channel-width scale, do not usually alter form in the short term, and are the basic structures comprising channel morphology that result from geomorphologic processes of erosion or deposition (e.g. rapids, pools).

At the time the study commenced, there were no structured definitions of biotope types beyond those refined by Wadeson (1994, 1996) and Padmore (1997) in parallel. Consequently, biotopes were defined visually on the basis of flow type and substratum composition, as per Appendix 3.3 (several biotopes commonly recognised by ecologists, e.g., cascades and glides, were absent from study reaches). During the course of the fieldwork, the biotope concept evolved, leading to a matrix of flow types and substrata as a basis for more consistent, standardised biotope identification and classification (Rowntree 1996). The definition of hydraulic biotopes remained based on the characteristics intuitively recognised by researchers and consistently used in this thesis, of: (1) flow type, describing the water surface appearance, which in turn has been shown to reflect more complex hydraulic conditions in the water column; and (2) substratum, which determines bed roughness, thereby directly influencing flow type, as well as fundamentally representing biotic habitat. Descriptions of the range of flow and substratum types agreed for hydraulic biotope identification are provided in Appendix 3.4.

Although there were differences between the classification adopted in this study and the finalised hydraulic biotope matrix, for pools and transitional biotopes, they were otherwise entirely comparable (see final column, Appendix 3.3). In this study, the 'pool' type was simplified by grouping pools spanning the full channel width with others located within the main channel, along channel margins or downstream of hydraulic refuges that altered hydraulics (i.e. obstructions or secondary flow cells), or in areas isolated from main channel flow. This was a useful grouping, in particular, in that very large cross-channel pools were uncommon, occurring mostly in the Riviersonderend reach. The Du Toits site possessed no distinct, main-channel pools, with marginal slackwaters representing the dominant low velocity biotope. In the biotope classification described in Rowntree (1996), pools and slackwaters were differentiated, with the former being in direct contact with upstream and downstream water, but with barely perceptible flow. In contrast, a slackwater was considered an area of no perceptible flow, hydraulically detached from the main flow but within the primary channel, that might occur at channel margins or mid-channel downstream of obstructions or secondary flow cells. Based on U.K. experience, in contrast, Padmore (1998) considered a pool to occupy the full channel width and exhibit scarcely perceptible flow, while a marginal deadwater had the same flow type but did not occupy the full channel width.

The other difference between the Rowntree (1996) biotope matrix and the types used in the current study was in relation to patches that might be hydraulically 'transitional' in nature, due to the spatiotemporal complexity of upper rivers in relation to discharge and channel morphology. Transitional biotopes were defined as areas that were difficult to visually categorise instantaneously in the field without hydraulic measurements, as they tended to fall between well-defined biotope types; only riffle-run and pool-run transitions were observed (Appendix 3.3). Wadeson (1996) similarly recognized a transitional biotope ('transition') at the run-riffle interface, as did a number of other researchers (Chapter 6). Although neither Rowntree (1996) nor Padmore (1998) identified transitional biotopes, they and King and Schael (2001) acknowledged that the boundaries among biotope types are indistinct, largely owing to the complexity of flow types and substrata falling within a single hydraulic biotope (see also Wang *et al*. 1996). In some instances, the classification of flow in rivers is based on altogether different factors than those considered in defining hydraulic biotopes. For instance, as Wadeson (1996) observed, the classification system of Davis and Barmuta (1989) hinges on the differentiation of near-bed rather than surface flow conditions. Unquestionably, additional work is required to achieve a consistent, international classification system.

Although all hydraulic biotopes in evidence at each site were included in reach-level biotope mapping (Appendix 3.3), only three key biotopes were selected for invertebrate sampling, namely riffles, runs and pools - the dominant biotopes studied to date (Wadeson 1996; Padmore 1997):

1. Riffles - included as typically the most speciose biotope type (Chapter 2), and often representing the areas where flow cessation and drying are first experienced with reduced discharge.
2. Runs - selected as the dominant biotope at all study sites, and a potential flow refugium (Section 1.4.4) for biota from other biotope patches with decreasing discharge.
3. Pools - included as they might be inhabited by taxa that are not particularly sensitive of low flow conditions, become increasingly dominant in areas as flow decreases, and provide last-resort refugia for taxa previously inhabiting riffles or runs.

It was envisaged that sampling invertebrates from these three biotopes would yield a wide range of hydraulic conditions inhabited by both flow sensitive and generalist taxa. Marginal and in-channel areas of damp substratum exposed with flow reduction were also mapped (unpubl. data).

Channel cross-section surveys: collection of data on hydraulic geometry, biotopes and point hydraulics

Selection of cross-sections

For each sampling trip, two cross-sections were surveyed in each location, for each site, within the template described in Section 3.4.1 (a total of 16 cross-sections per trip and an overall total of 96 cross-sections). Within each location, one cross-section was located across a width of channel predominantly representing riffle conditions and the other across a section dominated by run patches (Appendix 3.3), as indicated in Figures 3.2-3.5. Where possible, cross-sections were located so as to coincide with transects delimiting the

biotope map template, to minimize survey effort. Although the cross-sections were also used to calculate discharges (Section 3.2), adequate representation of the dominant hydraulic biotopes was the primary consideration.

Transect-level versus cell-level biotope assessment

Typically, there were few instances where riffle or run conditions spanned the full channel width, with most cross-sections traversing a range of patch types. For the purposes of this study, the term 'transect biotope' was adopted to reflect the dominant cross-channel biotope by proportion (Figure 3.7a). Patches within a transect biotope that reflected the same or other biotope types were referred to as 'cell biotopes', as illustrated conceptually in Figure 3.7b. In a parallel U.K. study of physical biotopes, Padmore (1997, 1998) similarly differentiated between transect and cell scales (with a cell representing the immediate location where hydraulic measurements were made); secondary, marginal and refugia biotopes were defined as patches within transect biotopes. Wadeson (1996) also identified the need for cell-wise classification of hydraulic biotopes rather than simply a classification at transect level.

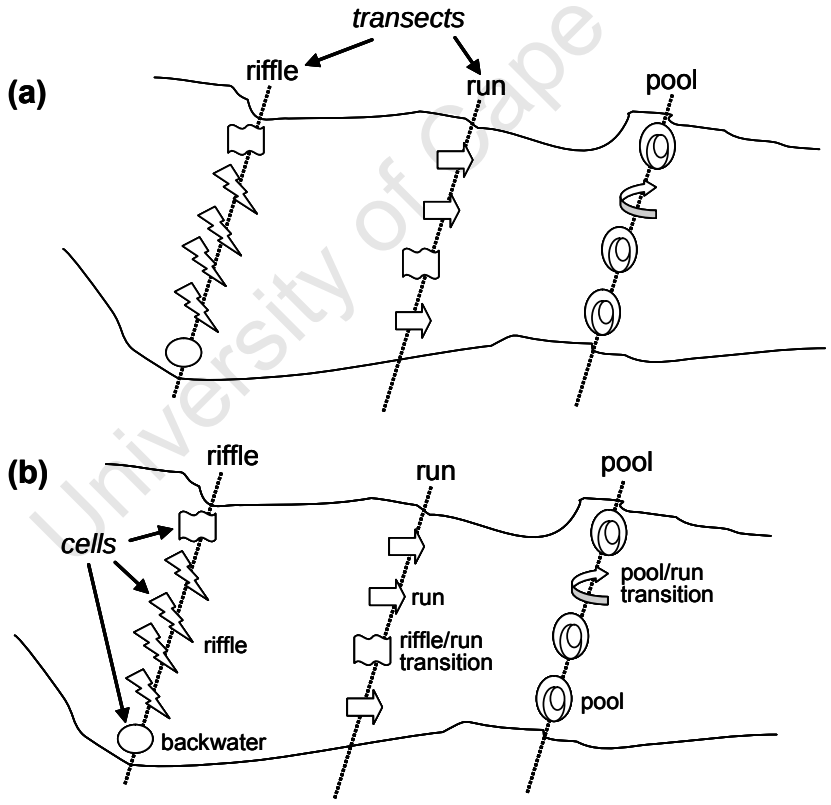


Figure 3.7 Schematic illustrating the identification of biotopes at (a) transect and (b) cell scales within a river reach (adapted from Padmore 1997). A transect biotope reflects the dominant biotope type across the full channel width, while within it other hydraulically different patch types or cell-level biotopes may be present, each illustrated here by different symbols.

Measurement procedures for hydraulic geometry, point microhabitat and biotope variables

For establishment of each cross-section, headstakes were secured in concrete as far from the wetted channel as possible, while still enabling adequate survey visibility, to allow for fluctuations in channel wetted width with flow. They were labelled according to specific survey codes, to include the site, bank and cross-section number (Appendix 3.2). For example, codes DUR1 and DUL1 indicate the headstakes for cross-section 1 on the right and left banks of the Du Toits River, respectively (Figure 3.4). Cross-sections 1 and 2 were located consistently in the control location and cross-sections 3 and 4 in the impact location, with numbering in a downstream direction (Figures 3.2-3.5). Headstakes were cross-surveyed to facilitate future re-establishment if needed. As far as possible, each cross-section was placed in the midst or towards the upstream end of the transect biotope, because in the case of riffles particularly, biotopes were liable to migrate hydraulically with fluctuations in discharge. At each cross-section, data on channel hydraulic geometry, hydraulic conditions at a series of dry and wetted points across individual cross-sections, and hydraulic biotope character were collected (Table 3.5); a simplified set of substratum measures was used, relative to the pilot survey. Wang *et al.* (1996) showed that such measurements of physical habitat were generally of high accuracy and moderate precision, but with both reduced in instances of high habitat heterogeneity.

Table 3.5 Overview of the main categories of physical habitat data collected in the field.

CHANNEL HYDRAULIC GEOMETRY (cross-sections)	POINT MICROHABITAT HYDRAULICS (cross-sections, sample microhabitat)	HYDRAULIC BIOTOPE CHARACTERIZATION (biotope maps, cross-sections, sample microhabitat)
Instantaneous discharge	Cell biotope type and transect proportions	Number of patches per biotope type
Stage	Water depth	Patch sizes and spatial arrangement
Elevation and chainage	Average and near-bed velocity	Percentage of biotope isolation from main channel
Wetted width	Turbulence	Biotope types represented by patches adjacent to the sampled biotope
Wetted perimeter	Substratum proportions, particle sizes, percentage embeddedness of sample stones in finer particles and corresponding substratum type	Possible change of hydraulic biotope type due to a previous discharge
Dominant biotope type	Proportions of silt, organic and inorganic detritus, algae and leaf litter covering and surrounding the substratum surface	
Degree of bed exposure	Upstream hydraulic refuges	
Gross morphological features	Percentage overhead and instream cover	
	Location and type of marginal and in-channel vegetation	

Fixed-point cross-section photographs were taken for each transect biotope and discharge. The survey tape horizontal distances from the headstake to each surveyed point were recorded, including to the locations of the waters' edges on the right and left banks (facing downstream). A series of 5-54 out-of-water and 11-34 in-water spot shots was surveyed across the channel to generate each cross-section profile (Table 3.5 and Appendix 3.5). Survey points were generally at evenly spaced increments, scaled according to reach width.

Points were located closer together near the (WEs of the channel both instream and on the bank, where the most obvious changes in wetted area with discharge were expected to occur. Additional wet points were included where distinct changes in hydraulic characteristics were apparent. Three to five WSEs were recorded across the channel (Appendix 3.5). Ratings were made of cross-sections of probable high or low accuracy of measurement. At each of the in-water survey points, depth, velocity and substratum condition, as well as related data, were recorded (Figure 3.8). Point data were similar to the microhabitat data recorded for stones from which invertebrates were sampled (see Table 3.5 and below).

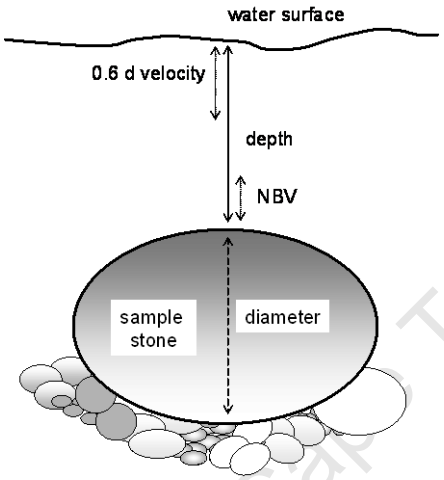


Figure 3.8 Schematic of hydraulic data measurement at each instream survey point.

Depth was measured to the nearest 0.01 m using the top-set wading rod of a Scientific Instruments Price AA current meter (Gordon *et al.* 1992). Average and near-bed velocities were measured using the calibrated current meter fitted with a standard AA or pygmy bucket wheel and the same top-set wading rod (Gordon *et al.* 1992). Bovee and Milhous (1978) considered the pygmy meter more appropriate for use for depths below 0.15 m, but limited to velocities below 0.90 m s^{-1}. Measurement of velocities at very low flows was problematic though (Section 3.2), and in most instances, slow and/or shallow flow conditions, as well as flow between large, closely spaced bed elements necessitated the use of the pygmy meter. This meter was also required in shallow areas of rapid flow, sometimes associated with high turbulence; three replicate readings were taken in such cases. Under conditions of natural, open channel flow, the typical vertical velocity distribution may be described using measurements of velocity at 0.2, 0.6 and 0.8 times the total water depth (d), measured from the water surface (Bovee and Milhous 1978; Gordon *et al.* 1992). Average velocity approximates that occurring at 0.6d, at depths below 0.75 m, under most flow conditions (Bovee and Milhous 1978). For this study, therefore, where water depths never exceeded 0.75 m, average velocity was routinely calculated using the one-point method (Equation 3.7) – recognising that vertical velocity profiles may break down under the variable or chaotic flow conditions commonly encountered in riffles (Carling 1992; Bouckaert and Davis 1998). Wadeson (1996) also noted a lower limit of 0.10 m for velocity measurement using this method. Depths sometimes fell below this limit at extreme low flows, doubtless

affecting the velocity profile and reducing measurement accuracy (Section 3.2). Calculation of average velocity using a four-point equation based on all three velocity measurements, is recommended in instances where there is an abnormal distribution of velocities, or when the 0.8d measurement is affected by obstructions or turbulence, as well as where time allows (Equation 3.8). Difficulties in velocity measurement at very low discharges (Section 3.2) and limits on sampling time precluded application of the four-point method, but it was used in the pilot study (Section 2.3). Near-bed velocity represented the current speed recorded directly above the substratum. As the meter itself required at least 0.06 m depth to function, where water depth was ≤ 0.06 m, near-bed velocity was assumed equivalent to average velocity. Where turbulence was audible or visually apparent during velocity measurement, this was recorded.

$$\bar{v} = v_{0.6d} \qquad \textbf{Equation 3.7}$$

$$\bar{v} = \frac{v_{0.2d} + v_{0.8d} + (v_{0.6d})}{4} \qquad \textbf{Equation 3.8}$$

Where:

$\bar{v}$ = average velocity (or mean water column velocity)
v_d = velocity at specified depth from the water surface
d = water depth

The presence of large bed elements located upstream of, but sufficiently close to the cross-section to be exerting an influence on downstream hydraulic conditions (Davis and Barmuta 1989) was recorded. For the first survey trip and for subsequent trips where additional survey points were required to address changes in hydraulic conditions with discharge, the percentage composition of the substratum for an area of 0.1 m^2 surrounding the survey point was visually estimated using a modified Wentworth substratum grade scale (Appendix 3.6). The dimensions of the stones representing each substratum category were recorded by measuring the α, β and c axes using a flexible 1-m tape (Figure 3.9). Other substratum features were also recorded (Table 3.5) and the hydraulic biotope (cell biotope; Figure 3.7b) represented by each surveyed point was categorized (Appendix 3.3).

Collection of point microhabitat data for invertebrate samples

For each grid-referenced (based on the location biotope map) stone from which an invertebrate sample was taken (Section 3.5), physical microhabitat data were collected in the same way as for points along each cross-section (Figures 3.8 and 3.9). A total of 864 sets of physical microhabitat data were collected, of which 144 corresponded with benthic macroinvertebrate data (Appendix 3.1). The types of data collected for each sample point are given in Table 3.5. Stone α, β and c axes were used to calculate sample surface areas (Section 3.5). Stone shape was rated on a 5-point scale (entirely round to entirely angular) and surface roughness on a similar 5-point scale (low (smooth) to high (strongly pitted/fractured). Stone surface

compactness, for the sample stone and the underlying substratum, was rated on the same 5-point scale as in the pilot study (Chapter 2) from low (easy to remove from the bed) to high (immovable). For the substratum underlying each stone, the percentages of the sample comprising various particle sizes were estimated (for each size category, the β axis of the minimum, maximum and median (d_{50}) size particle were measured). Percentages of inorganic and organic detritus, including leaf litter, associated with sampled stones were determined, as described in Section 3.5.

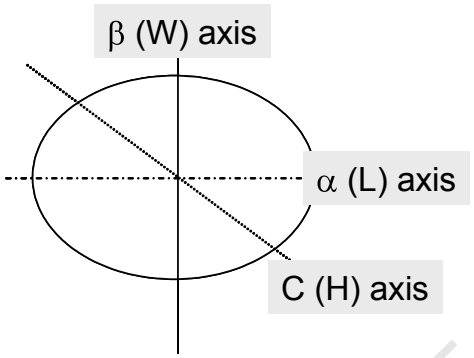


Figure 3.9 Schematic illustrating the three axes measured in the field for each sample stone to determine its substratum grade and surface area. W – width, L – length, H – height (in mm).

3.4.2 Analyses of channel hydraulic geometry

Relationships between hydraulic geometry and discharge were derived from cross-channel measurements across a range of discharges (e.g. Leopold and Maddock 1953; Gustard *et al.* 1987; Bragg *et al.* 1999), coupled with stage-discharge rating curves. Based on the surveys (Section 3.4.1) channel profiles were created for individual riffle and run cross-sections at each site location, with water surface elevations, and depth and velocity distributions, corresponding to trip discharges (Appendix 6.1). A stage-discharge rating curve (Gordon *et al.* 1992) specific to each cross-section was generated from profile data. Flow rating curves should be based on at least three discharge measurements spanning low and high stages (Newbury 1984). In this study high stage was relative, as the discharge range was narrow. As the water surface profile was often broken, a typical feature of pool and riffle sequences of mobile river beds (Newbury 1984), the mean WSE was used for individual transects. As the stage of zero flow was not always known, the rating function recommended in Birkhead and James (1998) could not be used. Instead, the best fit of a linear or non-linear relationship was determined using Excel 2000 - equations used for calculating trend lines are the same as those used for other hydraulic data and water chemistry analysis (Section 3.3). The use of different functions on a case-specific basis was considered acceptable, because there was no need to extrapolate the function beyond the data measured in the field and the discharge range was limited (A. Birkhead, Streamflow Solutions, South Africa, pers. comm.).

The basic cross-section data were used to assess changes in select hydraulic geometry variables within and among the different study sites, over the months encompassing the dry season, and in relation to observed discharges. In select cases, hydraulic variables were standardised to allow direct comparison among transect riffles and runs, and sites. Time series and hydraulics-discharge relationships were plotted for wetted channel widths (equivalent to 'top width'; Gordon *et al.* 1992), which were calculated from survey measurements, excluding and including any additional width due to patches of standing water along the channel margins. These patches made the clear demarcation of the full channel width difficult at all sites, due to the relatively weakly incised nature of the channels. Similar analyses were undertaken for riffle and run wetted perimeter (WP) - defined as the distance along the river bed and banks at a cross-section where they contact the water (Gordon *et al.* 1992). Wetted perimeters were calculated using the data on cross-section hydraulic geometry and best-fit stage-discharge relationships, using a hydraulic program developed by A. Birkhead. Although rectangular and triangular-shaped channel geometries should generate logarithmic and power relationships with discharge, respectively (Gippel and Stewardson 1998), channel form was variable at all sites and the discharge range narrow, so all potential functional relationships were explored. The hydraulic program was also used to ascertain changes in the degree of connectivity across the river bed, for riffle and run transects, with discharge fluctuations. The numbers of flowing or wetted sections interspersed with areas of exposed or drying substratum within the streambed (i.e. 'micro-channels', represented by the variable 'No. Ch.') were calculated. It was not possible to perform regression analysis on the degree of channel dissection with changes in flow, due to the bimodal relationship typically encountered, with high numbers of micro-channels occurring at both flow extremes.

Summary statistics also were calculated for the cross-sections, for the main hydraulic variables measured, namely depth, average and near-bottom velocity. The strengths of relationships between these variables and instantaneous discharge were determined using Excel 2000. An assessment of the proportion of wetted cross-section at or shallower than 0.05 m, and/or experiencing extremely low to zero flow conditions (average velocity ≤ 0.01 m s^{-1}) was also made. The derived variable, depth ≤ 0.05 m, was arbitrarily based on the fact that below 0.06 m, near-bottom and mean column velocities were effectively the same. The derived velocity variable, $v \leq 0.01$ m s^{-1}, was used to partition the river channel into flowing and non-flowing areas. Gippel and Stewardson (1998) indicated that such indices of habitat condition might have greater bearing on invertebrate flow requirements than standard depth and velocity measures.

3.4.3 Analysis of point microhabitat hydraulics

The point microhabitat data collected for stones from which invertebrates were collected (Section 3.4.1, Table 3.5), were used to calculate various hydraulic indices for objective classification of hydraulic biotopes (see below). Point hydraulics data were also essential for analysing biotope and microhabitat availability and suitability for different invertebrate taxa, as well as taxon hydraulic tolerances (Sections 3.5 and 3.6).

3.4.4 Methods for identification and flow-related characterization of hydraulic biotopes and analysis of biotope dynamics

To characterize hydraulic biotopes on the basis of discharge and to assess their spatiotemporal dynamics at individual sites at low flows, it was first necessary to establish the extent to which the field based, subjective identification of biotopes was valid. This was also an important step in understanding the extent to which flow related change in physical habitat could be represented by biotope dynamics, and ultimately, whether or not assessment maintenance of biotope character and diversity was an appropriate surrogate for invertebrate low flow needs. These steps were addressed through an objective biotope classification process, centred on discriminant function analysis, following biotope analysis at transect-level.

Assessment of biotope dynamics at transect scale

A first analysis of biotope patch dynamics with discharge was made at a coarse scale, using the proportions represented by different hydraulic biotopes (cells) across individual cross-sections (Figure 3.7a), at all site locations. Total wetted biotope length (m) and the length represented by individual biotopes were then calculated from recorded data on cell biotope type (Figure 3.7b) across each cross-section. Lengths representing exposed, dry sections of the channel were excluded from calculations. Results were converted to percentages of maximum biotope length, for riffle and run transects, and related to instantaneous discharge as percentages of maximum discharge, to allow inter-site comparisons. No objective assessment of biotopes was made at this scale, as the level of resolution of the results was considered inadequate for study purposes. Padmore (1997) corroborated this view in a similar study, demonstrating improved results in the classification of biotope flow types from analyses at the patch scale over the transect scale.

Description of hydraulic indices used in hydraulic biotope classification

For the purposes of objective biotope classification, a number of hydraulic indices were calculated based on field data (Table 3.5), from which set it was assumed certain indices describing mean and/or near bed flow conditions would exhibit the greatest capacity to differentiate among the biotopes defined *a priori*.

A number of studies have aimed to characterize the spatial and temporal heterogeneity of river flow environments associated with physical habitat on the basis of hydraulic indices (Section 1.4.8; e.g. Statzner *et al.* 1988; Davis and Barmuta 1989; Davis and Growns 1991; Wadeson 1996; Padmore 1997; Vadas and Orth 1998). The theoretical foundations of open channel hydraulics, on which the use of flow-based hydraulic indices as discriminators of habitat is based, are presented in Statzner *et al.* (1988), Davis and Barmuta (1989), Gordon *et al.* (1992) and Wadeson (1996). Commonly, lotic ecologists have focused their attention on hydraulic variables that strongly influence benthic invertebrates and are readily measurable at a sampling point, including depth, mean velocity and substratum size, to describe physical habitat (Newbury 1984; Section 1.4.8). This is exemplified, for example, in current procedures for physical habitat modelling within environmental flow research (Sections 1.5.5 and 3.6). These simple variables alone (referred to here

as 'core' variables) have been found inadequate to fully describe the complexities of flow hydraulics, and their scale dependencies may render comparisons among different size rivers or morphological features difficult (Wadeson and Rowntree 1998).

More complex, composite hydraulic indices describing both micro- and macro-flow conditions (or 'derived' indices) have been found to be of particular relevance in the flow-related classification of biotopes, functional mesohabitats and similarly defined habitats, as well as in understanding the potential ecological significance of such patches for biota (see below and Chapter 6). These indices, several of which are independent of scale, comprise two main groups (Statzner *et al.*1988; Davis and Barmuta 1989; Gordon *et al.* 1992; Wadeson and Rowntree 1998): (1) indices pertaining to the micro-flow environment near the river bed (e.g. shear velocity, roughness Reynolds number); and (2) indices relating to the mean flow component (i.e. the entire water column, e.g. Froude number, Reynolds number), which are relatively easy to derive, but do not directly consider the microenvironment in which many aquatic species reside. The derived indices described below were selected in addition to core ones, based on available literature, as of potential relevance in the flow-related characterization of hydraulic biotopes. A benthic shear stress index based on FST-hemispheres, trialled in the pilot study (Chapter 2), was not adopted despite being a good predictor of invertebrate distribution and abundance, because the procedure required major alteration of the natural hydraulic character of the bed for its measurement, and only partially characterized the near-bed flow environment (Bouckaert and Davis 1998). Although several authors have highlighted indices on the basis of their previously documented ability to discriminate among biotopes, most notably Froude number (see below), a broader range of indices was retained for this study.

Indices were calculated using a hydraulics data set of 1935 cases (Table 3.8) that covered all sites, locations, discharges, sampling months and biotopes identified in the field, including: (1) the hydraulic microhabitat data recorded at each of the points where invertebrates were collected (Sections 3.4.1 and 3.4.3) - a total of 872 cases (two cases with missing substratum data omitted); and (2) point hydraulic data recorded from cross-sections, for all cases where sufficient substratum data (required for the calculation of several hydraulic indices) were collected – a total of 1063 cases. In the latter set, cases where the substratum was bedrock dominated were omitted, as invertebrates were only sampled from cobbles/boulders. For the calculation of median substratum size, figures were based on the dominant substratum by area, or the greater particle size if equal proportions of two or more sizes were present, to best represent the influence of substratum on hydraulics.

Froude number

The Froude number is a complex, dimensionless hydraulic index (Equation 3.9) that can be used to describe flow conditions across different rivers, and at the reach or within-reach patch scale (Statzner *et al.* 1988). It represents the ratio of inertial to gravitational forces, the roughness of the water surface or near-surface turbulence, and, at shallow depths, also the turbulence of free flow (Statzner *et al.* 1988; Wadeson and

Rowntree 1998). The Fr value indicates whether flow is subcritical (i.e. tranquil or slow; Fr < 1), critical (Fr = 1), or supercritical (i.e. fast; Fr > 1) (Newbury 1984; Statzner *et al.* 1988; Davis and Barmuta 1989; Gordon *et al.* 1992). Higher values can therefore be expected in shallow-fast flowing areas, such as riffles (Vadas and Orth 1998). As Fr is independent of scale, Wadeson and Rowntree (1998) observed that large and small features are classified together if bulk flow conditions are similar, rendering it potentially powerful for biotope classification. The index has increasingly gained acceptance as a means of characterizing local scale habitat for the biota, and as a good predictor of flow types (Allen 1951, cited in Wadeson and Rowntree 1998; Statzner 1981a; Orth and Maughan 1983; Wetmore *et al.* 1990; Jowett *et al.* 1991; Davis and Growns 1991; Jowett 1993; Wadeson 1996; Yu and Peters 1997; Padmore 1997, 1998; Vadas and Orth 1998; Kemp *et al*. 2000; King and Schael 2001; see also Chapter 6).

$$Fr = \frac{v}{\sqrt{g\,d}} \qquad \textbf{Equation 3.9}$$

Where:
v = mean column (0.6d) velocity (m s^{-1})
d = water depth (m) (equivalent to *L*, characteristic length, often taken as the hydraulic depth)
g = acceleration due to gravity (9.81 m s^{-2})

Reynolds number

The Reynolds number (Re) is a complex hydraulic index of the ratio of inertial to viscous forces and thus, water-column or free-flow turbulence (Statzner *et al.* 1988; Davis and Growns 1991; Gordon *et al.* 1992; Wadeson and Rowntree 1998; Vadas and Orth 1998). Depending on the relationship between these two forces, flow may be defined as laminar, turbulent or transitional. As Wadeson (1996) noted, flow is laminar if viscous forces are so strong relative to inertial ones that viscosity plays a significant part in determining flow behaviour, and turbulent if viscous forces are weak relative to inertial forces. The point of transition between laminar and turbulent flow is represented by the critical Reynolds number, 2000 (Gordon *et al.* 1992). Values for Re from 500-2000 represent laminar or partially turbulent flow in open channels, while larger values indicate turbulence (Gordon *et al.* 1992). Consequently, highest Re values are to be expected in faster, deeper areas (Vadas and Orth 1998).

$$Re = \frac{v\,d}{\nu} \qquad \textbf{Equation 3.10}$$

Where:
v = mean column velocity (m s^{-1})
d = water depth (m) (equivalent to *L*, characteristic length, often taken as the hydraulic depth)
ν = kinematic viscosity of water (approx. 1 x 10^{-6} m^2 s^{-1} for water at 20 °C)

Aquatic invertebrates are known to experience the full range from laminar to turbulent conditions throughout their lifetime, from Re values around 1-10 (and even lower) to figures of 1000 or higher when they are adults (Statzner 1988). Laminar flow may also exist in the river as a laminar sublayer, the arguable implications of

which for the benthos are discussed extensively in Gordon *et al.* (1992). According to Statzner *et al.* (1988), as Re is dimensionless it is appropriate at reach and patch scales. Wadeson and Rowntree (1998) stated, however, that it is of limited use for comparing biotopes across a range of scales, due to its scale dependence (as a product of depth and velocity). They observed though that the degree of turbulence reflected by Re may be a suitable indicator of shear forces acting on the river bed and within the flow, and hence, Re might be a useful descriptor of hydraulic conditions as experienced by lotic organisms. Wadeson (1996) and Wadeson and Rowntree (1998) used Re as one of several discriminatory indices in biotope classification (Chapter 6).

Velocity:depth ratio

The ratio of velocity to depth has been used as a key hydraulic variable in physical habitat description by several authors, including Jowett (1993), Wadeson (1996), Wadeson and Rowntree (1998), and Vadas and Orth (1998) (Chapter 6). The latter authors identified it as a turbulence index that should be highest in shallow-fast (riffle) areas.

$$VD_{ratio} = \frac{v}{d}$$ **Equation 3.11**

Where:
v = mean column velocity (m s^{-1})
d = water depth (m)

Shear velocity

Statzner *et al.* (1988) considered shear velocity (v_*) a complex hydraulic index characterizing near bed flows within or for an entire river reach. Velocities close to the river bed are far lower than those in the water column, due to the frictional resistance created by the stationary bed. The index generates the force acting on the river bottom known as shear stress, and is a measure of that stress expressed in velocity units (Statzner *et al.* 1988; Davis and Growns 1991; Gordon *et al.* 1992). In rocky streams, v_* generally approximates one tenth of the mean velocity, due to differences in relative roughness (Davis and Barmuta 1989). In the present study, shear velocity was used in lieu of shear stress based on FST-hemispheres (Chapter 2). The equation for shear velocity at a point was applied (Equation 3.12), as the most practical of the various formulae available, given the limited water depths and variable bed topography (Statzner *et al.* 1988; Wadeson 1996; Wadeson and Rowntree 1998); it also is not possible to determine energy slope values on a point-by-point basis. Shear velocity was used as a biotope descriptor by Wadeson (1996), Padmore (1997), and Wadeson and Rowntree (1998).

$$v_* = \frac{v}{5.75 \log_{10}(12d / k_v)}$$ **Equation 3.12**

Where:
v = mean column velocity (m s^{-1})

d = water depth (m)
k_v = substratum roughness height = d_{50} (m)

Roughness Reynolds number

Roughness Reynolds number (Davis and Barmuta 1989; Davis and Growns 1991; Gordon *et al.* 1992; Wadeson 1996), also referred to as boundary Reynolds number (Statzner *et al.* 1988; Vadas and Orth 1998), is a complex, dimensionless hydraulic index relevant at both river reach and patch scales. In a similar way to viscous sublayer thickness, it can be considered an approximate indicator of turbulence conditions close to the river bottom (Statzner *et al.* 1988). Similar to relative roughness below, the index can be used to determine the extent to which the boundary is hydraulically smooth (i.e. surface irregularities are so small that they are totally submerged in the laminar sublayer) or rough (i.e. the roughness height extends above the laminar sublayer and affects the flow outside it) (Wadeson and Rowntree 1998). A surface is considered hydraulically smooth if $Re_* < 5$, hydraulically rough if $Re_* > 70$, and transitional for the range $5 < Re_* < 70$ (Schlichting 1961, cited in Wadeson and Rowntree 1998). The index has the potential to be an excellent habitat descriptor, according to Davis and Barmuta (1989), since it combines the effects of substratum type and velocity. Vadas and Orth (1998) noted that as a measure of bottom turbulence, highest Re_* values should be found in shallow-fast (riffle) areas with coarse substrata. It was used to characterize hydraulic biotopes by Wadeson (1996) and Wadeson and Rowntree (1998).

$$Re_* = \frac{v_* k_v}{\nu} \qquad \textbf{Equation 3.13}$$

Where:
v_* = shear velocity (m s^{-1})
k_v = substratum roughness height = d_{50} (m) (i.e. the effective height of the irregularities that form the roughness elements)
ν = kinematic viscosity (m^2 s^{-1})

Relative roughness index

Relative roughness (R_{rel} or R) represents the ratio of the roughness height to the hydraulic radius (i.e. depth relative to the height of the substratum element; Gordon *et al.* 1992). Hydraulically rough conditions, where the roughness height extends above the bottom laminar sublayer, affecting outside flow, are prevalent in rivers. However, hydraulically smooth flow can occur in instances where surface irregularities become very small in comparison with water depth.

$$R_{rel} = \frac{k_v}{d} \qquad \textbf{Equation 3.14}$$

Where:
k_v = substratum roughness height (m)
d = water depth (m)

According to the literature, substratum roughness height (k_v) may be calculated in various ways, and tends to be subjectively defined by individual researchers on the basis of the prevailing grain size distribution, as well as in some cases, on the orientation of particles on the river bed and the extent to which they project into the flow. For example, Statzner *et al.* (1988) and Wadeson (1996) calculated k_v using data derived from substratum profile samplers. Commonly, some characteristic diameter of streambed materials, such as d_{50} or d_{85} is used to approximate k_v (Gordon *et al.* 1992), despite the fact that there is not necessarily a correlation between particle diameter and substratum roughness (Davis and Barmuta 1989; Wadeson 1996). Vadas and Orth (1998) applied the lower third of values for the substratum size range, rather than average particle size, to account for oblong, flat particles with limited protrusion into the water column. In the present study, the diameters of the median particle size within a range (d_{50}) or of single individual stones sampled for invertebrates were used as representative k_v values. Wadeson (1996) explored the extent to which R_{rel} showed a pattern of hydraulic variability among biotopes, but did not apply the index beyond a preliminary analysis. In contrast, Padmore (1997) used the index more extensively in biotope classification (Chapter 6).

Velocity shelter index

A turbulence index, velocity shelter (VS), formulated to differentiate runs and fast riffles from deeper pools, and applied by Vadas and Orth (1998), uses the difference between mean column velocity and near-bottom velocity (NBV) as a measure of degree of shelter for biota. In their study, demersal velocity was measured 0.045 m above the bottom. Near-bottom velocity was measured at a similar height above the bed in this study, so difference in the two velocity measures were negligible for very shallow waters. Moreover, there were 292 instances where VS was negative, indicating greater velocities closer to the streambed than at 0.6 depth from the surface, due to shallow depths at low discharges or chaotic flow (Davis and Barmuta 1989). A high value for the index typically indicated a higher degree of shelter from high velocities close to the river bed, given that near-bottom velocities were most often lower than average conditions, except in cases of localised turbulence as a result of bed friction.

$$VS = v - NBV \qquad \textbf{Equation 3.15}$$

Where:
v = mean column velocity (m s^{-1})
NBV = near-bottom velocity (m s^{-1})

Relative exposure index

The dimensionless relative exposure index developed and applied by Padmore (1997) to determine whether or not flow types could be distinguished from a non-velocity based index, was also used in this study for biotope characterization. An equivalent index, the 'relative submergence index', was used as a measure of turbulence in visual classification of mesohabitat types by Vadas and Orth (1998). Effectively, in this study, the index represented the inverse of R_{rel}. As a measure of the relative protrusion of substratum elements into the water column, Vadas and Orth (1998) noted that it should be highest in deeper pools with fine substrata.

$$RE = \frac{d}{k_v}$$ **Equation 3.16**

Where:
d = water depth (m)
k_v = substratum roughness height = d_{50} (m)

Turbulence index

A turbulence index, TI, developed and thus far applied only by Padmore (1997) in a study of physical biotopes, was also employed in the present study. Considered a good possible predictor of flow types and biotopes at high discharges and for cross-river comparisons (although it is not truly dimensionless) by Padmore (1997), the extent to which it might be similarly useful at low flows remained to be tested.

$$TI = d\,(v / k_v)$$ **Equation 3.17**

Where:
d = water depth (m)
v = mean column velocity (m s^{-1})
k_v = substratum roughness height = d_{50} (m)

The shelter index of Padmore (1997), calculated as SI = (s/1000)/Fr, where s = particle diameter (mm), could not be applied in this study, due to 294 cases of Fr values of zero in the data set. This limitation was unfortunate in that the index was purportedly developed as a discriminator between low and drought flow types that could be applied across different rivers.

Objective characterization of hydraulic biotopes

Discriminant function analysis is an exploratory multivariate technique that can be used to determine which variables discriminate best between two or more naturally occurring groups, and to enable the classification of cases (StatSoft 2001). It was used here to provide a statistically objective test of the extent to which the subjective field-based identification of hydraulic biotopes was meaningful, specifically at low flows. The groups were the hydraulic biotopes identified *a priori* in the field, on the basis of dominant flow type and substratum composition (Appendix 3.3).

Forward stepwise discriminant analysis was used to develop models of which hydraulic indices made the most significant unique (additional) contribution to the discrimination among hydraulic biotopes, based on *F* values. Tolerance values (defined as 1-R^2, and based on the multiple correlations for each variable with all other variables) were used to exclude indices with a high degree of redundancy relative to those variables already included in the model (and hence, with questionable contribution to improved discriminatory power). For each model developed, the Wilks' lambda statistic denoted the statistical significance of the model's discriminatory power. With a range in value from 1 (no discriminatory power) to 0 (perfect discriminatory power), the closer to zero the value calculated, the greater the discriminatory power. Partial Wilks' lambda

figures indicate the independent contribution of the respective hydraulic index to overall discrimination among hydraulic biotopes (essentially equivalent to the partial correlation coefficients of multiple regression analysis). The lower the partial Wilks' lambda, the greater the additional discriminatory power provided by the variable. Although lambda values can be converted to corresponding *F* and *P* levels, these are approximate. Furthermore, selecting only those indices shown to be significant is considered inappropriate, in that chance is being capitalized upon when multiple indices are included without *a priori* hypotheses (StatSoft 2001).

Canonical correlation analysis generated the discriminant functions that detailed how the various hydraulic indices in the model discriminated among biotopes (StatSoft 2001). Different independent (orthogonal) discriminant functions (canonical roots) were computed, where each successive one contributed less to overall discriminatory power. Those discriminant functions found to be statistically significant, based on a Chi square test of successive roots, as well as computed standardised coefficients for the canonical variables and canonical means, for the significant functions, were used to interpret which hydraulic indices contributed most in each instance and in what manner (based on the positive or negative sign of each root). Also considered were the eigenvalues for each discriminant function and the cumulative proportion of explained variance accounted for by each one. Factor structure coefficients, representing the correlations between the hydraulic indices and the discriminant functions, were consulted for further interpretation of discriminant functions.

Classification of subjectively identified individual cases (samples in the field) among hydraulic biotopes, with objective allocation according to the discriminant functions already defined, was undertaken to ascertain the general robustness of the designated biotope types. It also demonstrated the degree of difficulty in subjective identification of discrete patches in the field and highlighted the biotopes most commonly confused as a result. *A priori* probabilities that a case belonged to a certain biotope were proportional to group sizes. The resultant classification matrix indicated the percent of cases that were correctly classified in each biotope by the calculated classification functions – these differ from discriminant functions in that they are computed for each group and can be used to directly classify a case into the group for which it possessed the highest classification score. The matrix also indicated the number of misclassified cases per biotope and how they were misclassified. Importantly, the classification is *post hoc*, as opposed to a means of *a priori* predictive classification. Although it is possible to use the classification matrix predictively, by classifying new cases, this was not an objective of this study. The actual classifications for each case, in conjunction with squared Mahalanobis distances from group centroids (i.e. a measure of the distance between each case and the group centroid defined by the respective group means for each hydraulic index) and posterior probabilities were used to ascertain the reasons for misclassifications.

Discriminant analysis, including classification, of hydraulic biotopes using the suite of hydraulic indices described above was performed at three levels, for the data sets outlined in Table 3.6. Summary statistics of

hydraulic variable per biotope type and box-whisker plots for select analyses were examined alongside the results obtained. Although overall, the F-test within ANOVA is robust to deviations from normality and to heterogeneity of variances (Lindman 1974, cited in StatSoft 2001), and all hydraulic indices showed normal distributions (Kolmogorov-Smirnov test), for the majority of indices the assumption of homogeneity of variances was not met (Levene's test). Therefore, Kruskal-Wallis ANOVA by ranks was used preferentially, where required, to test for significant differences in hydraulics among groups. Mann-Whitney U tests were used to identify which group pairs were most responsible for any differences observed. The U test is the most powerful (sensitive) nonparametric alternative to the *t*-test for independent samples; in certain instances, it may offer even greater power to reject the null hypothesis than the *t*-test. Moreover, with samples larger than 20, the sampling distribution of the U statistic rapidly approaches the normal distribution. Results from standard ANOVA and *post hoc* unequal N HSD tests generally corroborated results.

(1) Aggregate data set

Analysis of the entire data set ('aggr'), grouping data from all recorded biotopes, from all sites (and locations), across the entire range of discharges measured, provided a first understanding of which hydraulic indices were the most powerful discriminators among different hydraulic biotopes, which of them best described individual biotopes, and which hydraulic indices, if any, were redundant. Separate analyses were conducted to explore the relative power of core versus derived hydraulic indices, or a combination, in discriminating among biotope types and, thereby, identifying hydraulically unique biotopes. In most instances the indices used were dimensionless, readily allowing comparison across different discharges and sites. Although it is acknowledged that the inclusion of the core indices (depth, average and near-bed velocity, and substratum as d_{50} particle size) introduced elements of site and discharge dependency, the sites were established as sufficiently geomorphologically and hydraulically similar at the outset of the study (Chapter 2) for generalized analyses to be considered useful. A further analysis using pooled data explored the extent to which the two transitional biotopes identified in the field (viz. riffle/run and pool/run transitions; described in Appendix 3.3) were discrete biotopes or merely reflected the difficulty in visually identifying areas of water near patch boundaries (and of assigning boundaries to what might be a natural hydraulic continuum). The final analysis explored any changes in model robustness and classification ability when only the three main biotopes (riffles, runs and pools) from which invertebrates were sampled (Section 3.6), were examined.

(2) Low flow classes

A key objective of the discriminant analysis was to ascertain whether biotopes maintained their hydraulic character across all low flows or exhibited discharge-dependency. Such information was considered central in understanding the extent to which biotope-level response to flow might be used as a surrogate for the biota in characterizing invertebrate low flow requirements. Separation of the data set into low flow classes was done objectively, through examination of the flow percentiles represented by individual discharges on site

annual FDCs (Chapter 4). The classes were identified irrespective of month, because different rivers displayed natural differences in the timing of the month of lowest or highest discharge. The classes adopted were as follows:

- 'high' - The higher end of the range of low flows most often associated with the onset of autumn (April-May) or early summer (December), was differentiated by flow percentiles below Q_{80}. All sites except the Elands had cases in this flow class for these months. The flows in this class are elevated low flows and do not represent fresh or flood events.
- 'natl' - The 'normal' range of dry season flows was classified as $\geq Q_{80}$ and $< Q_{99}$. The class contained only cases representing natural discharges. For the Elands site only, all cases fell within this flow class.
- 'extl' - Extreme low flows were characterised by percentiles $\geq Q_{99}$. This class encompassed only the data for experimental locations at sites during the impact phase (i.e. there were no cases representing natural low flows).

(3) Sites

Finally, it also was considered important to establish the extent to which hydraulic biotopes maintained their hydraulic character irrespective of river site, at low flows. If large-scale differences in biotope hydraulic character or in the ability to objectively classify biotopes were evident among sites, it would point to limitations in the generalized use of biotope-low flow relationships among different rivers.

Table 3.6 Maximum numbers of cases examined in the discriminant function analyses for biotopes, sites and discharges, and in aggregate total.

BIOTOPE	NO. CASES	SITE	NO. CASES	DISCHARGE CLASS	NO. CASES
Riffle	590	Elands	566	Higher	583
Riffle/run transition	124				
Run	763	Molenaars	452	NatLow	1165
Trickle run	11				
Pool/run transition	86	Du Toits	435	ExtLow	187
Pool	336				
Backwater	14	Riviersonderend	482		
Standing water	11				
Total	**1935**		**1935**		**1935**

Biotope patch dynamics, numbers and diversity at reach scale

Assessments of reach-scale biotope dynamics with discharge magnitude were based on the biotope maps for individual site locations (Section 3.4.1). The corresponding survey data were downloaded by DWAF survey personnel and basic surveying calculations performed the program Survey Assistant. Preliminary plots of the maps were created using Model Maker and Ultimate Map Maker (CAD) programs. Data loss by DWAF

precluded cross-linked digitisation of all biotope maps (as illustrated in Figure 3.6) for GIS-based calculation of biotope proportions, as well as the determination of advanced spatial metrics. Hence, biotope data were calculated only from freehand maps, using a counted-squares procedure on standard graph paper. For each site location, three maps were selected representing as widely different discharges possible (including an impact survey). The additional maps representing the extreme flow situations for the three experimental locations were also assessed – in all, 27 maps were analyzed. The planar surface area of each reach (location) was estimated from its total length multiplied by its average wetted width (including areas of standing water). Areas of reach that were physically affected by the constructed diversion weirs were excluded from original calculations (four maps only), but all results were then standardised to 60 m reach length for comparisons. The numbers of patches (irrespective of size) and areal extent of each patch were determined for the different biotope types mapped at each location. All eight visually identified biotopes were treated separately, based on the results of objective classification (Chapter 6). Coarse estimates were also made for instream and exposed (with discharge reduction) vegetation including algae, and patches of exposed substratum of different size classes.

Analyses of flow-related biotope dynamics were based on:

1. The relationship between the proportion of total planar area occupied by different biotope types and discharge.
2. Changes in the number of individual patches, both in total (i.e. irrespective of assigned biotope) and per biotope type (pool, run, trickle run, etc.), with discharge. The first of the two indices is similar to the biotope 'patchiness' index adopted by Padmore (1997, 1998), and an index of habitat spatial heterogeneity.
3. Changes in hydraulic biotope 'diversity' with discharge. The index used is comparable to that used by Padmore (1997, 1998), with diversity simply defined as the number of biotope patches discerned for a given reach length multiplied by the number of biotope types (of a maximum of seven possible types). In this study, the full 60-m extent of each location was used and patch numbers were standardised by division by average channel width, where necessary, to account for the different sizes of the study rivers. Also, where appropriate, discharges were standardised by Q_{50} from the corresponding annual FCD percentile for each site, to enable inter-site comparisons. In contrast, Padmore (1997, 1998) used a site length of 10 channel widths and flow percentiles to account for differences in river scale. The biotope 'diversity' index adds biotope type as a further dimension to habitat heterogeneity for the biota.

The Hydraulic Biotope Diversity Index (HBDI) and associated curves based on cumulative frequency rankings, devised by Rowntree and Wadeson (1996), were not adopted for this study, but provided an alternative means for comparing results (Chapter 6). Padmore (1998) believed that more sophisticated biotope indices were not feasible until such time as additional ecological information on biotopes was generated.

3.4.5 Site and biotope substratum conditions

Information on substratum conditions, quantified on a point-wise basis along cross-sections (Section 3.4.1), was used to describe the substratum character of locations and biotopes, as well as to provide measures for certain hydraulic equations (Section 3.4.4). Records were made in December when discharges were relatively high and, therefore, proportions of silt and other fines lower than at the peak of the dry season (pers. obs.). Substratum conditions were compared in all instances on the basis of graphical analysis of percentage composition of different mineral (Appendix 3.6) and non-mineral classes. Data on stone size, in particular, for the stones from which invertebrates were collected (Section 3.4.3), comprised a key aspect of the analyses described in the next section.

3.5 METHODS OF DATA COLLECTION AND ANALYSIS FOR BENTHIC MACROINVERTEBRATES

3.5.1 Methods of data collection

Field sampling and laboratory methods for the collection of invertebrate and related environmental data (e.g. epilithic detritus, freshwater algae) are outlined in this section. For each sampling trip, at each site and location, and for riffles, runs and pools, three replicate benthic macroinvertebrate samples were taken from individual stones (Appendix 3.1). Specific biotopes and microhabitats were sampled in order to obtain hydraulics that properly reflected invertebrate microdistributions (Davis and Barmuta 1989). Individual samples from the same biotope type typically were taken from different patches within the riverbed landscape. Sampled stones ranged in size from large gravel to large cobble (*c.* 64-256 mm diameter; Appendix 3.6), with the majority of samples collected from small cobbles (> 64-128 mm). For each stone, the invertebrate sample was separated into three parts, as illustrated in Figure 3.10, namely: (1) top of stone (T); (2) bottom of stone (B); (3) substratum underneath the stone (U). Sampling invertebrates from individual stones is reported to yield more precise estimates, per unit effort, of diversity and density than Surber sampling (Death 1991, cited in Death and Winterbourn 1995), but the inherent difficulty of accurately sampling parts of a stone (Boulton *et al.* 1988) is acknowledged.

The stone top was routinely sampled first, by scrubbing the stone surface and collecting invertebrates using either a small or large 80 µm-mesh, hand net with a terminal collecting bottle (designed by the author) held directly over and downstream of the stone, or a box sampler. A suite of physical microhabitat variables were then collected (Section 3.4.3). A medium-sized box sampler with 80 µm-mesh collecting bottle was then put in place around each stone, which was carefully lifted and its bottom surface area scrubbed. The substratum underlying each stone was sampled immediately afterwards, using either the hand net or a modified, 80 µm-mesh small box sampler (designed by the author). The surface of the substratum that had been directly in contact with each stone was scrubbed, providing a semi-quantitative sample part (Figure 3.10). In contrast, 'T' and 'B' parts of the stone sample were quantitative, according to surface area (Figure 3.10 and Appendix 3.7). For each stone, the most appropriate combination of sampling devices was selected prior to sampling,

depending on stone position and size. All sampled stones were rechecked once they had fully dried out, to ensure that any invertebrates utilizing stone grooves/pits as refuges from desiccation were accounted for. Stones were painted post-sampling, to eliminate the possibility of re-sampling a stone where the assemblage was still recovering from a previous sampling episode; invertebrate recovery times for small patches within greater undisturbed areas of river bed have been found to range from a single day to around 38 days (Yount and Niemi 1990). While sampling was during daylight hours, it is acknowledged that differences in microdistribution patterns might be obtained or biases minimized, through 24-hour observations of substratum-invertebrate associations (e.g. Glozier and Culp 1989; Johnson and Covich 2000).

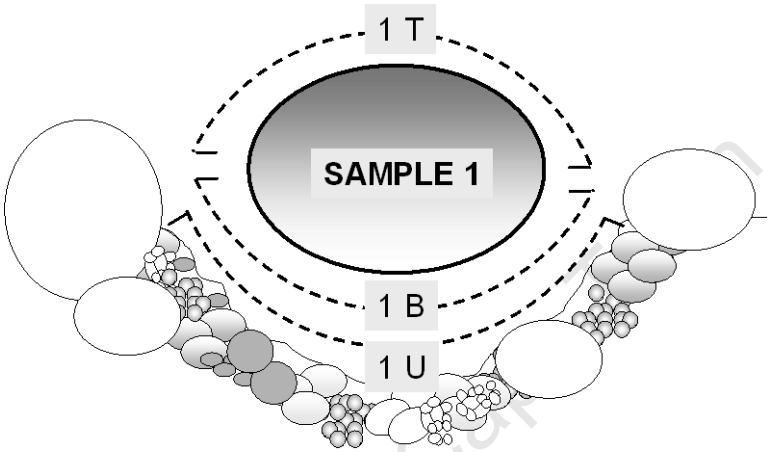


Figure 3.10 Schematic illustrating the division of each sample stone into three separate sample parts from which benthic macroinvertebrates were collected. Sample 1 is divided into: 1T - top stone surface; 1B - bottom stone surface; 1U – the surface of the substratum underlying the stone.

The invertebrate data set comprised a total of 432 samples, where each sample comprised a top (T), bottom (B) and underneath (U) part (a total of 1296 parts; Appendix 3.1). Invertebrates collected from the three stone parts of each sample were stored in separate collecting bottles, preserved in a mixture of 8% buffered formalin diluted to 4%. On return to the laboratory, the samples were transferred to 70% ethanol for long-term preservation. For each sample part, all invertebrates were picked from the organic detritus, identified to the taxonomic level of family or higher taxon, and counted, using a Nikon stereo dissecting microscope. A subset of 1008 sample parts was identified and analyzed at family-level (only a subset of U parts, excluding those of pools, was used; Appendix 3.1). Invertebrate keys consulted included: Usinger (1956); McCafferty and Provonsha (1981); Scott (1983); Cranston *et al.* (1983); Wiederholm (1983); Merritt and Cummins (1984); Scholtz and Holm (1985); Harrison (2000); Day *et al*. (2002); De Moor *et al*. (2003a, b); and Picker *et al.* (2004).

Although the focus was at family level, select analyses were conducted at species level using the Chironomidae (a dominant family at all sites) as a target group. The family encompasses a wide range of species expected or known to exhibit different microhabitat requirements, life history patterns, and responses

to flow (Chapter 7). A subset of the complete data set was examined, comprising the December, February, March and April samples from all three biotopes. For the pool biotope, only the T and B parts of each sample were identified to species level, for all four months. All three sample parts were examined for riffles and runs for all trips except March (when only T and B parts were identified to species level). The majority of chironomid identifications were made or confirmed by an international expert (A.D. Harrison); pupal exuviae and adults collected at each site were used as an aid. For all species, a unique reference catalogue number was assigned and permanent slide mounts were prepared. A chironomid collected from the Du Toits River, which represented a new genus and species, *Paradoxocladius mangoldi* (Orthocladiinae), is described in Harrison (2000).

Quantification of samples based on unit stone surface area

To enable quantitative comparisons of invertebrate abundances among samples and stone parts, numbers of individuals of each taxon were standardised to 0.1 m^2 unit surface area, based on a regression equation developed for local stone surface areas (see Appendix 3.7). The surface areas of the top and bottom parts of each sample stone were then calculated on the assumption that the two parts were always equal in area for standardisation (Figure 3.10). For the purposes of simplification, the surface area of part U of the sample was assumed to be of the same size as T or B, as only the upper surface of the underlying substratum directly covered by each sample stone was sampled. However, invertebrate data from part U of each sample were regarded as semi-quantitative, in that the accurate surface area would be partially dependent on substratum composition and particle size distribution.

Surface area of part T/B/U = 0.5 x whole stone surface area **Equation 3.18**

Organic detritus associated with biotopes

For the individual parts of each invertebrate sample (Section 3.5), for a selection of sampled stones from each biotope, per location and sampling trip, an assessment of the percentage of organic and inorganic detritus was made once all invertebrates had been removed. A total of 114 whole-stone samples was analyzed for riffles (52), runs (32) and pools (35). For sample parts, data were compiled for different biotopes for 41-68 stone tops (T), 44-63 bottoms (B) and 29-51 areas representing underlying substratum (U). In each instance, all of the detritus, ranging from fine particulate organic matter and silt to coarse detritus, including leaves, was combined, placed in a muffle boat and dried in an oven at 60 °C to constant weight (total dry mass, DM_{total}). Samples were then pre-weighed, combusted in a muffle furnace at 450 °C for 5 hours to burn off all organics and re-weighed to calculate the dry mass ($DM_{organic}$) and percentage represented by the organic fraction ($\%_{organic}$).

Algal collection and surveys from biotope maps

Where algae were observed on field trips, samples were collected and returned unpreserved to the laboratory for specialist identification (P. Joska, Botany Department, UCT). The relative proportions of algae within each reach, and algal condition, were visually estimated in the field (as was also done for macrophytes).

3.5.2 Methods of analysis of benthic macroinvertebrate data

Spatiotemporal changes in faunal composition in relation to biotope type and low flow regime

The program suite PRIMER Version 5 (Clarke and Gorley 2001), developed for non-parametric, exploratory and statistical analyses of multispecies and environment data, was the principal means by which patterns in invertebrate distribution and abundance were explored across and within hydraulic biotopes, and in relation to low flows (Chapter 7). In other instances, ANOVA and non-parametric analogues were utilized to examine inter-group differences, including taxon-biotope associations, as described in Zar (1984) and StatSoft (2001) (Chapters 7 and 8). For certain analyses, the Chironomidae were used as a potential indicator family to explore species-level habitat specificities and responses to low flows.

Classification and ordination

Multivariate classification and ordination of invertebrate data were based on normal q-type analysis (Field *et al.* 1982; King and Tharme 1994, p. 194, Figure 8.2). Using the PRIMER program, CLUSTER, benthic macroinvertebrate abundances (per 0.1 m^2) were first fourth-root transformed (Equation 3.23). This fairly severe transformation was used to downweight the importance of very abundant taxa so that the less dominant, and even rare ones, played some role in determining similarity levels between samples (Clarke and Warwick 2001). It also functioned to reduce right-skewness and to stabilise variance. For some subsets of analyses, transformation to only presence/absence was used.

Fourth-root transformation:

$$Yij = \sqrt{\sqrt{Xij}} = Xij^{1/4} \qquad \textbf{Equation 3.19}$$

Where:
X_{ij} = raw data score of the *i*th species in the *j*th sample
Y_{ij} = corresponding transformed score

The basis for the classification (and subsequent ordination) was a Bray-Curtis similarity matrix computed from the *s* taxa by *n* samples array (Equations 3.20 and 3.21). The Bray-Curtis similarity coefficient is invariant to changes in measurement scale and unaffected by joint absences in the data set (Clarke and Warwick 2001).

Bray-Curtis dissimilarity measure:

$$\delta_{jk} = \frac{\sum_{i=1}^{s} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}$$ **Equation 3.20**

Where:
Y_{ij} = score for the *i*th species in the *j*th sample
Y_{ik} = score for the *i*th species in the *k*th sample
δ_{jk} = dissimilarity between the *j*th and *k*th samples summed over all *s* species; δ_{jk} ranges from 0 (identical scores for all species) to 1 (no species in common), and is the complement of the similarity S_{jk}

Bray-Curtis similarity measure:

$$S_{jk} = 1 - \delta_{jk}$$ **Equation 3.21**

Group-average linking of the Bray-Curtis similarities was employed in CLUSTER, where two groups of samples are joined at the average level of similarity between all members of one group and all members of the other, which considers natural variability between samples (Clarke and Warwick 2001). Although dendrograms, the outputs of such hierarchical agglomerative classification, have the advantage of clustering samples into discrete groups, the cut-off levels for groupings are arbitrary. There are also several disadvantages to this approach which make it advisable to employ an additional method of presentation of the group relationships (Field *et al.* 1982):

1. Once a sample has been placed in a group its identity is lost.
2. Dendrograms show only inter-group relationships and the sequence of samples in a dendrogram is arbitrary, with two adjacent samples in a group not necessarily being the most similar.
3. Dendrograms tend to over-emphasize discontinuities and may, therefore, artificially force a continuum or graded series into discrete classes.

Consequently, as recommended in Field *et al.* (1982) and Clarke and Warwick (2001), clustering analysis was used in conjunction with ordination. Superimposition of the clusters obtained from dendrograms at various levels of similarity on corresponding ordination plots enables inter-group relationships to be re-assessed on a continuous scale. Furthermore, agreement between the two forms of data representation lends support to the consistency and adequacy of both methods in describing assemblage relationships.

The non-metric, multidimensional scaling (MDS) method of ordination was performed using the PRIMER MDS program, considered one of the best ordination methods available (Clarke and Warwick 2001). The principles of the method are described in Shepard (1962, cited in Clarke and Warwick 2001) and Kruskal (1964, cited in Clarke and Warwick 2001). In the context of sample analysis, the purpose of non-metric MDS is to construct an ordination of the *n* sites, in a specified number of dimensions, by interpreting some

function of the dissimilarity measure (rank order) between each pair of sites as Euclidean distance. It is an iterative procedure where a starting map of the *n* sites is constructed in the required number of dimensions, and the configuration is perturbed in a direction which decreases the stress (Equation 3.22) to an acceptable global minimum. Multiple repeats of the analysis are performed to ensure convergence to a global, as opposed to a local, minimum stress. The inter-point distances of the configuration are then regressed on the corresponding dissimilarities using a general monotonic transformation to distance. The MDS is non-metric in that the regression is non-parametric, making few assumptions about the data and allowance for the typically non-linear relation of dissimilarities to distance encountered in biological data (Field *et al.* 1982). Similar samples are located close together and highly dissimilar ones far apart in the resultant ordination plot. An inherent limitation of the method is that greater weight is placed on large distances, so as to emphasise overall assemblage structure (Clarke and Warwick 2001).

The goodness-of-fit of the regression was assessed using a Shepard diagram, illustrating distance against dissimilarity, for all pairs of values in the plot, and the corresponding stress value (Equation 3.22), which totals the scatter around the regression. Stress provides an indication of the distortion involved in compressing the data to typically two dimensions (for ease of interpretation); low stress indicates that the sample relationships are well represented by a plot of the sites in the specified dimensionality (Field *et al.* 1982). The following general rule was applied:

- Stress < 0.05 provides an accurate representation of the data with no prospect of misinterpretation.
- Stress < 0.1 gives a good ordination with misleading interpretation being unlikely; higher-dimensional solutions will not add to the overall structure of the plot, although the fine structure of compact groups may benefit from closer examination. At stress levels below 0.1, the ordination is considered a more useful representation of the data than a dendrogram.
- Stress < 0.2 corresponds to a potentially useful 2-d ordination with misleading interpretation being unlikely; interpretation of the plot should be made with caution, as well as reference to the results using an alternative method (e.g. classification).
- At higher stress values (stress > 0.2), increasingly less reliance should be placed on a 2-d plot, and it may become necessary use higher-dimensional ordinations to improve the representation of relationships, and/or alternative approaches.

Stress formula:

$$\text{Stress } 1 = \sqrt{\frac{\sum_{j}^{n}\sum_{k>j}^{n}\left(d_{jk} - \hat{d}_{jk}\right)^2}{\sum_{j}^{n}\sum_{j>k}^{n} d_{jk}^{\,2}}} \qquad \textbf{Equation 3.22}$$

Where:
n = number of stations

d_{jk}: k > j; j = 1, ...n = interpoint distances between *j*th and *k*th stations of the configuration (ordination plot), which are then regressed on the corresponding dissimilarities (δ_{jk})

$\hat{d}_{jk}$ = distance estimated from the regression, corresponding to dissimilarity, δ_{jk}

Analysis of similarities

The analysis of similarities (ANOSIM) test (PRIMER 5) provides a means of statistically supporting assemblage patterns generated using multivariate exploratory techniques such as classification and ordination (Clarke and Warwick 2001). It is a non-parametric analogue of MANOVA (which is almost always invalid for typical taxon-abundance matrices, according to Clarke and Warwick 2001) that makes no distributional assumptions about the data and is used to test for significance differences between groups of samples specified *a priori*. Although it lacks sensitivity compared with a MANOVA test, its greater generality is considered to adequately compensate for this limitation. The R test statistic reflects the observed differences among sites, contrasted with differences among replicates within sites. It ranges between R = 1, only if all replicates within sites are more similar to one another than any replicates from other sites, to R = 0 where the null hypothesis (H_o) is true and similarities among and within sites are the same, on average. In addition to indicating whether or not the calculated differences are significant, the R statistic provides a comparative measure of the degree of site separation. Comparison of the observed R value with a simulated distribution of R values for a null hypothesis of 'no site differences', generated by a randomisation procedure, shows whether or not the true R value falls outside the distribution, and hence, allows rejection of H_o. If only *t* of the T simulated values of R are as large as or greater than the observed R, then H_o can be rejected at a significance level of:

$$\frac{100\,(t+1)}{(T+1)}\ \% \qquad \textbf{Equation 3.23}$$

Following a global R test, ANOSIM similarly can be used for pairwise multiple comparison tests, although the risk of drawing a Type I error compounds markedly with decreasing sample replication (e.g., there is a risk of a 10% error with three replicates). The degree of risk of a Type II error cannot be ascertained, and it can only be stated that statistical power will improve with increasing replication (Clarke and Warwick 2001).

Identification of potential discriminant taxa among sample groups

For the groups of samples identified as differing significantly from one another using ANOSIM, the program SIMPER (PRIMER 5) was used to identify the taxa primarily responsible for the observed differences. It computes the average Bray-Curtis dissimilarity between all pairs of inter-group samples, and then breaks the average down into the separate percentage contributions to dissimilarity made by each taxon. It was also used to a lesser extent to compute the contributions of individual taxa to the average Bray-Curtis similarity within a group. The ratio of the average contribution from the *i*th taxon ($\overline{\delta}_i$) to group dissimilarity and corresponding standard deviation, SD (δ_i), was used to identify any potential discriminant (indicator) taxa.

For such taxa, the ratio is large, indicating that the taxon contributes both considerably and consistently (across all samples) to the inter-group dissimilarity. Similarly, using the same ratio based on similarity ($\overline{\delta}_i$ / SD (δ_i)), species that typify a group were identified (Clarke and Warwick 2001). Taxa were ordered in decreasing contribution to dissimilarity (or similarity), and a recommended similarity cutoff of ≤ 50% was used to identify the major contributors.

Trends in invertebrate diversity at low flows and among biotope types

The PRIMER program, DIVERSE, was used to calculate five common univariate indices (all logarithms base *e*) as measures of attributes of assemblage structure that reflect, in a condensed form, the way in which the total number of individuals in a sample is divided up among the different taxa. Washington (1984) provides a review of diversity indices. Two different aspects of assemblage structure contribute to the concept of diversity (Clarke and Warwick 2001):

1. Species/taxon richness, which is a measure of the total number of species/taxa.
2. Equitability or evenness, which expresses how uniformly the numbers or individuals are distributed among the different species/taxa. The converse of evenness is dominance, where a sample exhibiting a high degree of dominance will possess low evenness.

The Shannon-Wiener diversity index (*H'*) was used, because it a common index in disturbance studies that incorporates both the richness and equitability components of community diversity (Clarke and Warwick 2001). Although *H'* is known to be an underestimate of the diversity in a sampled population, the bias decreases with increasing sample size (Bowman *et al.* 1971, cited in Zar 1984). In addition to the total number of taxa (effectively species density - number of species per sample/unit area; McCabe and Gotelli 2000), taxon richness was calculated using Margalef's index (*d*), a measure of the number of species/taxa present for a given number of individuals, which, thus takes account of both the total number of taxa/species (*S*) and the total number of individuals (*N*). The validity of applying similar rarefaction corrections to account for the sensitivity of species density to total abundance, which may be altered with flow disturbance (e.g. Fisher *et al*. 1982; McCabe and Gotelli 2000), is acknowledged. A commonly used index of equitability, Pielou's evenness index (*J'*) was also calculated, with taxon dominance reflected in 1 - *J'*. Relative strengths and deficiencies of these measures are discussed in Washington (1984), Magurran (1988) and McCabe and Gotelli (2000).

Shannon-Wiener diversity index (*H'*):

$$H' = -\sum_i p_i (\ln p_i) \qquad \textbf{Equation 3.24}$$

Where:
p_i = proportion of the total count arising from the *i*th species/taxon

Margalef's species richness index (*d*):

$$d = \frac{(S-1)}{\ell n\, N} \qquad \textbf{Equation 3.25}$$

Where:
S = total number of species/taxa
N = total number of individuals

Pielou's evenness index (*J'*):

$$J' = \frac{H'(observed)}{H'_{max}} \qquad \textbf{Equation 3.26}$$

Where:
H'_{max} = maximum possible diversity which would be achieved if all species/taxa were equally abundant $(\ell n\, S)$

Trends in individual diversity measures in relation to month (i.e. season and temporal sequence of flows), location and biotope type, (Chapter 7) and discharge magnitude (Chapter 8) were examined using two-way ANOVA coupled with *post hoc* Tukey HSD tests. Results were corroborated using a non-parametric analogue (Kruskal-Wallis ANOVA by ranks) to address the high ranges in diversity indices for some samples, especially at extreme flows. Analyses for trends in diversity for individual biotopes at sites were restricted to pairwise comparisons of means across months based on summary statistics; paired t-tests for comparisons of diversity for biotopes during the impact phase, as well as their non-parametric equivalent, were considered unreliable due to small sample sizes (n = 3; StatSoft 2001) and associated non-homogeneity of variances (Levene's test results). The discreteness and degree of similarity among riffle, run and pool biotopes, in terms of individual diversity indices, were also explored through single-factor ANOVA, followed by Tukey HSD tests. Samples from only control locations were pooled to eliminate possible effects of experimental treatments in some months, as well as to ensure a balanced design, for all sites for the entire low flow period. For just the impact phase (both months combined), for control versus impact locations, paired t-tests for independent samples by groups were used to identify biotope-specific impact effects. All three experimental sites were grouped to represent flow reduction below natural minima (Chapter 4), thereby combining any effects on biotope diversity of varying extremes of discharge reduction across impact locations.

Invertebrate tolerances for changes in habitat hydraulics at low flows

Although species traits were not examined in relation to low flow disturbance (e.g. Townsend *et al*. 1997b), attention was paid to the characterization of taxa as habitat-flow specialists or generalists on the basis of their tolerances to low flow hydraulics. Relationships between invertebrate taxa at sites and the various hydraulic

indices used to characterize different biotopes at low flows, as well as taxon tolerance ranges, were first explored using correlation analysis and summary statistics (Chapter 8). More focused examination of tolerance levels to flow-related changes in hydraulic habitat, for select flow-indicator families and chironomid species, was based on the construction and comparison of microhabitat suitability index (HSI) curves (as used in the PHABSIM component of IFIM; Section 1.5.5) for key hydraulic variables (Chapter 8).

A wide range of approaches have been used to examine invertebrate microhabitat using habitat suitability curves. In the incremental method (Gore and Judy 1981; Gore 1987, 1989), habitat suitability curves are derived from the fit of a third or, commonly, fourth order polynomial equation to plots of cumulative mean numbers of individuals, as a function of increments in hydraulic conditions. In alternative exponential polynomial curve models, an interactive depth-velocity term is included, to account for hydraulic interdependencies (Gore and Judy 1981; Morin *et al*. 1986; Gore 1987, 1989; Mathur *et al*. 1985; but cf. Statzner *et al*. 1988; Paxton 2000). Polynomial regression on a single factor (Orth and Maughan 1983) is similar to the incremental method, but with log-transformation of observed densities prior to curve construction to minimize variance, and subsequent fitting of independent polynomial regression models relating species density to each habitat variable. Multiple regression has also been applied (Gore and Judy 1981, but see Statzner *et al*. 1988), where log-transformed densities are expressed as a linear or polynomial function of all selected habitat variables (the effect of a single variable is isolated by holding the other variables constant). A critique of aspects of these methods is provided in King and Tharme (1994); see also reviews provided in Morin *et al*. (1986), Gore (1987), Statzner *et al*. (1988), Slauson (1988) and Paxton (2000).

In this study, selection of flow indicator families and species (Bovee *et al.* 1978) for curve development was based on the following criteria: a strong correlation with highly flow-responsive hydraulic variables; continued presence of the taxon at extreme low flows; a clear association with one of the dominant hydraulic biotopes; and conservatively, at least 30 observations of habitat use at natural low flows (Bovee 1986; Bovee and Zuboy 1988; Thomas and Bovee 1993). Curves for a species population typically can be well described using 20 samples (Statzner *et al*. 1988, 1990). Category II habitat utilization curves and category III habitat preference curves (*sensu* Bovee 1986) were created, and contrasted with the availability of different hydraulic conditions. Habitat utilization curves were created to reflect the microhabitat conditions actually utilised by the target taxon. Preference curves take into account any bias associated with the fact that optimal conditions might not have been available at the site (i.e. due to limited microhabitat availability, by also including conditions where the taxon was not recorded) to show true microhabitat preference. Bovee (1986) outlines the procedure for combining habitat availability and utilization data sets to generate preference curves (see also King and Tharme 1994).

Frequency analysis (Bovee 1986; Slauson 1988), the most frequently applied of all available methods, was used in this study to generate HSI curves because of its relative simplicity, lack of assumptions (e.g.

regarding the modality of response; cf. several methods listed above) and flexibility (e.g. in relation to treatment of curve tails). It also has been demonstrated to produce the least error of several techniques evaluated (Cheslak and Garcia 1988). Details of this approach, and of its strengths and limitations, are provided in King and Tharme (1994), as well as in Bovee and Cochnauer (1977), Bovee (1986), Gore (1987) and Bovee and Zuboy (1988). Essentially, the sum of taxon abundance counts was plotted for each size-class increment of the hydraulic variable, in histogram form. An envelope curve was drawn that best described the functional relationship between the taxon and the hydraulic habitat variable of concern, with the region of the curve exhibiting the greatest incremental increase in abundance, normalized between zero (zero suitability) and one (maximum suitability), effectively representing the most suitable range of the particular variable. As curve shape can be influenced by the choice of class interval (Morhardt 1986), a modified Sturges equation was used as a guide in selection of optimum class intervals (Cheslak and Garcia 1988). Data smoothing was not required, as suitability trends were clear from the raw data (Slauson 1988; Cheslak and Garcia 1988). Utilization and preference curves were ended at their upper tails simply at the midpoint of the last class interval for which measured data were available, while lower curve endpoints were set based on whether or not the target taxon could be expected to utilize zero values (Slauson 1988; King and Tharme 1994). Preference curves were somewhat affected at the upper ends by lower counts of high taxon densities in higher classes, because availability data tended to be more limited at higher hydraulic values. Conversely, at their lower tails the curves were skewed, due to the prevalence of non- and slow-flowing areas at very low flows.

Data were pooled across the biophysically similar sites (Chapter 2) and across months, with care taken to minimize potential biases by ensuring appropriate data standardisation (see Locke 1988). Potential limits to the transferability of habitat suitability criteria across rivers were taken into consideration (Bovee 1986; Morin *et al.* 1986; Gore 1987; Thomas and Bovee 1993; Groshens and Orth 1994). Although the select hydraulic factors were examined separately, their probable interdependencies in influencing habitat selection (Gore and Judy 1981; Statzner *et al*. 1988; Gore and Nestler 1988) are acknowledged. Suitability criteria were classified following Groshens and Orth (1994) as: optimal (SI value ≥ 0.7), marginal (SI value > 0 to < 0.7) or unsuitable (SI value $= 0$). It was recognised that habitat suitability data collected in sub-optimal habitat areas should be used with caution (Orth 1987; Tharme 1996). The assumptions that the observed habitats include the taxon's preferred ones and that optimal habitats are used proportionally (i.e. that the highest densities of individuals occur in the most preferred habitat) (Johnson and Covich 2000) were accepted. It is noteworthy that the SI curves cannot be interpreted as probabilities of occurrence with a taxon expected to be found with certainty at locations exhibiting the modal level of occurrence of a habitat variable, when in reality, taxa can only be expected to be found at locations within the range of their use of the particular habitat variable (Moyle and Baltz 1985; Shirvell 1986; Scott and Shirvell 1987). Moreover, as discussed in King and Tharme (1994), the curves provide little indication of the actual worth of that habitat; for instance, on two different sampling occasions, the maximum number of a species corresponding to a

particular habitat variable may be different, but the rating will be 1 (optimal) in both cases (Mathur *et al.* 1985).

Linking invertebrate assemblages to patterns of biophysical conditions at low flows

The PRIMER program BIOENV was used to link invertebrate assemblages to ecologically meaningful, multivariate environmental patterns at natural and extreme low flows (Clarke and Ainsworth 1993; Clarke and Warwick 2001). The degree of agreement in pattern is measured using a comparison of the similarity ranks, using Spearman (ρ_s) or weighted Spearman (ρ_w) rank correlation coefficients, for the (dis)similarity matrices underlying both the biotic (Bray-Curtis similarity, see above) and abiotic (normalised to Euclidean distance) ordinations. Results from BIOENV were used to identify the combinations of physical habitat and water chemistry variables yielding the greatest degree of concordance with faunal assemblage patterns (i.e. the abiotic variable subset maximizing rank correlation between the biotic and abiotic matrices), and hence, premised to be most relevant in structuring invertebrate assemblages across hydraulic biotopes at low flows.

The more robust companion program, BVSTEP, which undertakes a similar optimization search in a stepwise, more hierarchical manner (adding or deleting variables one at a time), and utilises fixed starting proportions of variables, was used for preliminary analysis of relationships between riffle assemblages and environmental patterns for the full pilot study data set, due to the large number of variables involved. It was followed by BIOENV for select subsets of variables (Chapter 2). With searches for best variable combinations where the number of variables is greater than approx. 15, BVSTEP is a more appropriate approach (Clarke and Warwick 2001).

Multiple regression analyses of diversity indices and flow-indicator taxa against a suite of measures of physical habitat, chemistry variables and discharge, also were employed in characterizing ecologically meaningful low flows for invertebrates. Adjusted R^2 values were reported, to account for the number of regressors and degrees of freedom. It was acknowledged that in the occasional cases of small sample sizes, there was an increased possibility of elevated high type I or type II error rates (Feminella 1996).

Invertebrate response to low-flow disturbance history

Identification of the best subsets of flow indices for examining invertebrate response to low-flow disturbance history was based both on analysis of the group affinities of individual flow variables based on PCA (Section 3.2.3; Chapter 4) and simple linear regression of flow indices, from different temporal windows, against individual taxon densities; Clausen and Biggs (1997, 2000) adopted similar approaches for the identification of ecologically relevant flow indices. Additionally, BIOENV analysis was used to identify which combination of flow indices independently, or in combination with variables reflecting reach habitat and chemistry, were most influential in structuring invertebrate assemblages.

4. LOW FLOWS AND DISTURBANCE: IDENTIFICATION OF HYDROLOGICAL INDICES OF POTENTIAL ECOLOGICAL RELEVANCE

4.1 INTRODUCTION

Stimulated by the growing body of theory and empirical evidence explicitly connecting river hydrology and ecology (Section 1.4) substantial advancements continue to be made, particularly since the 1990s, in characterizing flow regimes for ecohydrological purposes (Jowett and Duncan 1990; Poff and Allan 1995; Richter *et al*. 1996, 1997a; Poff 1996; Poff *et al*. 1997; Clausen and Biggs 1997, 2000; Puckridge *et al.* 1998; Arthington *et al*. 2006; Olden and Poff 2003; Monk *et al*. 2006, 2007; Konrad *et al.* 2008). Indeed, even early on, Gustard (1979, p. 53) and Poff and Ward (1989), among others, proposed a more rigorous description of river flow regimes specifically because it might enable "closer links between hydrology and biology to be identified". Although a diverse range of approaches have emerged to assist hydrologists and ecologists in more usefully quantitatively describing river flow character and relationships between long-term hydrological data and aquatic biota, as described below, a lack of appropriate tools for ecohydrological assessments remains a constraint. Moreover, as McMahon and Finlayson (2003) observed, if biologists rather than water resource hydrologists had developed the majority of methods used for hydrological analysis, the suite of techniques would have been quite different.

4.1.1 Ecohydrological characterization of river flow regimes: purpose and scale

Individual rivers or groups of rivers possess distinctive patterns of hydrological variability (i.e. 'hydrographic signatures', *sensu* Puckridge *et al.* 1998) that drive their ecological character (Section 1.4.2) and thus, in large part, their biophysical responses to flow-related physical disturbance (Section 1.4.4). Such streamflow variability is manifest over a range of temporal and spatial scales, from an inter-annual to a diel basis. Low flows are an integral part of the natural flow regime and its flow variability (Humphries and Baldwin 2003), alongside high flow events, with each river exhibiting a particular low flow pattern (Gustard and Bullock 1991; Stanley and Fisher 1992; Uys and O'Keeffe 1997b; Tharme and King 1998; Agnew *et al.* 2000; Lake 2000; McMahon and Finlayson 2003; Humphries and Baldwin 2003; Section 1.4.2). Importantly, flow regulation may reduce such natural variability at one scale, but increase it at another (Puckridge *et al.* 1998).

The historical flow record represents an invaluable, flexible source of information in describing, in ecologically meaningful terms, the spatial and temporal patterns of variability and disturbance in different

lotic systems, providing fine- to coarse-grained hydrological descriptors to match study scale (Poff and Ward 1989; Levin 1992; Poff and Allan 1995; Poff 1996). Certainly, understanding a river's flow disturbance history in terms of the temporal distribution or regime of hydrological extremes, is central to comprehending biotic response to flow change (Covich *et al*. 2003; Section 1.4.4), though "the temporal resolution in hydrological data required to characterize a stream's disturbance regime adequately is not clear" (Poff 1996, p. 72).

A hierarchical approach, that considers the multiple temporal or spatial scales of a river's hydrological character, is essential for the description and comparative assessment of hydroecological variability (Thoms and Parsons 2003; Biggs *et al.* 2005; Poff *et al*. 2006a, b). Attempts have been made to group individual rivers in terms of their hydrological attributes and hence, by implication, expected patterns of behavioural response in relation to flow disturbance, from global, to regional and local scales (Poff 1996). Haines *et al*. (1988), Tharme and King (1998), Puckridge *et al*. (1998), and Naiman *et al*. (2002) all held the reservation that although attempts to classify rivers into hydrological groups or types had considerable merit at varying scales, some generalizations might be too simplistic in that every river has its own characteristic flow regime and associated biotic communities.

Puckridge *et al.* (1998) differentiated three scales of hydrological character within which the ecological implications of flow variability could be considered. They proposed the term 'flow pulse' for the first temporal window, defining the pulse as a rise and fall in discharge (or stage) at scales of space and time appropriate to the observer's frame of reference. It was felt that biological response to a flow pulse might be at the population dynamics level, but apparent as behavioural or physiological responses during the event. The flow pulse tends to viewed from a flood perspective, incorporating micro-scale influences generally persisting less than a year (Junk *et al.* 1989; Thoms and Sheldon 2000; Thoms and Parsons 2003). The second window of 'flow history' represents the sequence of pulses occurring before any point in time, characterized by changes in population or community dynamics (Puckridge *et al.* 1998), incorporating flood and drought sequences (i.e. meso-scale influences between 1-100 years; Thoms and Sheldon 2000; Thoms and Parsons 2003). The third temporal window, 'flow regime', was intended to represent the long-term statistical generalization of the hydrograph, reflecting macro-scale influences that occur over hundreds of years (Puckridge *et al.* 1998; Thoms and Parsons 2003), and with responses reflected in the evolution of life history strategies (Walker *et al*. 1995; Lytle and Poff 2004). Thoms and Sheldon (2000), for example, examined hydrological change in the Barwon-Darling River, Australia, at pulse, history and regime scales of hydrological behaviour, using a range of summary statistics reflecting low to high flow characteristics and overall variability. Similarly, Thoms and Parsons (2003) used a multivariate statistical approach to identify spatial and temporal patterns in the hydrological character of the Australian Condamine-Balonne River, relating observed patterns to scenarios of water-resources development. Arthington and Pusey (2003), in addressing hydrological alteration effects on rivers comparably distinguished among, but with differences in temporal scale: the flood pulse, operating over a period of days to weeks; flow history, representing a time

period of weeks to years; and flow regime, over a time span exceeding decades. In this thesis, 'flow disturbance history' broadly encapsulated these various scales.

Classification of hydrological regimes

Large-scale characterization of flow regimes has largely depended on the examination of hydrological data within annual, seasonal or monthly time frames (Poff *et al*. 2006a), although more recent studies have utilized daily flow data (e.g. Hughes 1987; Poff and Ward 1989; Hughes and James 1989; Jowett and Duncan 1990; Richards 1990; Poff 1996; Clausen and Biggs 1997, 2000). Poff (1996) demonstrated that for ecological applications, daily hydrological data provide important information that is not apparent when flow records are analysed at coarser scales. The majority of regime classification studies have addressed overall flow variability, investing often disproportionate effort in describing high flow attributes as widely recognized agents of river disturbance (Sections 1.4.3, 1.4.4 and 7.1). Characterization of low flow regimes has been more limited (e.g. regional drought analyses), with few studies exploring low flow attributes in any depth from a physical disturbance perspective.

Several researchers have attempted to describe and compare the hydrological regimes of rivers across broad geographies, classifying rivers into hydrological groups or types on the basis of a wide range of flow and related features. Haines *et al*. (1988), at the global scale, identified 15 flow regime types in an analysis based on patterns of variability in mean monthly flows. Poff *et al*. (2006a) examined hydrological variability at a multi-country scale, using 463 sets of daily streamflow data from five continents. They found similarities in hydrological characteristics across countries, on the basis of a suite of 66 ecologically relevant flow indices (i.e. IHA statistics – Section 1.5.3), despite intercontinental differentiation based on streamflow variability. Using data for five American rivers spanning a continental gradient of hydroclimatic variation, they also demonstrated that flow variability was influenced by spatial domain and geomorphic setting, from basin to reach scales. Poff *et al.* (1996b) similarly found numerous regional differences in hydrologic response when they examined patterns of flow regime variation along various land-use gradients for 158 catchments within four large U.S.A. hydrological regions, as well as pre- to post-dam patterns of flow alteration for 43 of the streams. Ten ecologically relevant flow metrics were used in the study, reflecting flow magnitude, frequency and duration. Richards (1990) undertook a regional hydrological classification of 118 tributaries of the North American Great Lakes, based on cluster analysis of seven measures of flow variability and event responsiveness, as well as discriminant analysis to identify combinations of flow variables that optimally identified river cluster membership.

Joubert and Hurly (1994) undertook a general hydrological classification of South African rivers, which Uys and O'Keeffe (1997b) later complemented with a descriptive classification of flow regime types for the country's wide range of perennial to intermittent rivers. A study of the low flow regimes of 1350 rivers of northwest Europe, reported in Gustard and Gross (1989, cited in Smakhtin 2001), showed that the spatial variation in low flows exceeded that of flood measures. Consistent relationships were found within the

region between the mean and variability of annual minima and low flows of different durations, as well as between the magnitude of annual minimum flows and variability of low flows. Gustard (1979) outlined hydrograph analyses of over 500 U.K. rivers that provided the basis for objectively defining both low and high flow disturbances to the natural flow regime at sites downstream of reservoirs, and Gustard and Bullock (1991) further characterized local low flow regimes. Englund and Malmqvist (1996) differentiated among the flow regimes of three groups of 51 river sites in North Swedish rivers, namely unregulated, regulated (i.e. altered flow pattern, but unreduced discharge) and reduced flow sites (average of 96% discharge reduction), using 11 different variables related to flow magnitude and variability. Mader *et al.* (1997, cited in Bragg *et al.* 2005), developed a typology of 11 classes for Austrian rivers, based on indices of flow variability (viz. the ratio of mean monthly discharge to mean annual discharge, and ratios for bimonthly flow minima and maxima).

Nathan and McMahon (1990b) applied multiple regionalisation approaches to identify hydrologically homogeneous regions, for the prediction of low flow characteristics, using data from 184 catchments in southeastern Australia. Hughes (1987) undertook a hydrological regionalization for 77 Tasmanian rivers, deriving four hydrologically distinct groups of rivers on the basis of 12 flow indices that addressed flow variability, at annual as well as monthly low flow and peak flow scales. Hughes and James (1989) generated five hydrologically distinct regions in Victoria, Australia, from a hydrological regionalization of 138 stream gauge sites, based on 16 flow variables. They considered their attempt at a more specific classification of the rivers' low flow regimes ecologically unusable, because it failed to produce a geographically homogeneous regionalization pattern, with the four groups dispersed throughout the state (but see Campbell 1992, and Section 4.5.3).

4.1.2 Identification of ecologically relevant flow indices in the context of response to hydrological disturbance

Streamflow metrics are often used as surrogates for disturbance (e.g. Hughes and James 1989; Poff and Ward 1989; Poff 1996; Clausen and Biggs 2000) with "variations in discharge at any spatial or temporal scale are likely to be significant for at least some organisms" (Puckridge *et al.* 1998, p. 55; Poff *et al*. 2006a). Unfortunately, in the past, many of the flow indices used in ecohydrological studies have been selected arbitrarily, without consideration of their potential ecological relevance, though such relevance is clearly paramount (see Section 1.4.2). As Poff (1996, p. 72) stated, "hydrological analysis can provide information useful to ecologists and managers only if *ecologically relevant* aspects of the hydrological regime are identified and analysed and then put into a geographical context". Puckridge *et al.* (1998) too indicated that hydrological analyses should be based on the biologically significant facets of the flow regime, observing that such a need has been expressed repeatedly, but seldom met. This deficiency has been particularly apparent in environmental flow studies where single (low) flow indices, often used to rapidly determine minimum flows for biota (Section 1.5), have been criticised for their inflexibility, inability to reflect natural

flow variability, and lack of ecological relevance and credibility (Tharme 1996, 2003; Petts *et al.* 1996; Richter *et al*. 1996, 1997a; Arthington *et. al*. 2006).

Many different flow statistics can be used to describe the hydrology of a river, but clearly some possess more ecological merit than others (Poff and Ward 1989; Whittington 2000). Although many of the flow indices currently used in predictive ecohydrological modelling of biophysical responses to flow disturbance are somewhat arbitrarily selected, there has been a deliberate, concerted transition from the use of single hydrological indices that tend to emphasise average flow conditions, to a multivariable approach to hydrological characterization that reflects flow regime variability and holds greater potential for ecological relevance. For a flow metric to be ecologically relevant, it should be known to have, or reliably be extrapolated from ecological principles to have, some demonstrated measurable ecological influence and hence, will be important in assessing ecological responses to hydrologic alteration (Arthington *et al*. 2006, Monk *et al.* 2007). An aim of this thesis was to identify such ecologically substantiated hydrological indices for invertebrates, for low-flow disturbance (Section 1.2).

The availability for use of suites of flow indices that describe multiple facets of a river's flow regime has paved the way for potentially more meaningful ecohydrological characterization of flow regimes, but as several authors have observed "a difficulty for stream ecologists is choosing appropriate flow variables from the plethora that are available to represent such components of the flow regime" (Olden and Poff 2003; Clausen and Biggs 2000, p. 186). As a result, a vast collective of competing, oftentimes redundant, flow indices has been used to characterize river hydrological regimes (as discussed in: Poff and Ward 1989; Poff 1996; Puckridge *et al.* 1998; Clausen and Biggs 2000; Olden and Poff 2003). Olden and Poff (2003) identified 171 such flow indices used in ecohydrological studies. Clausen and Biggs (2000) noted that over 50 different flow variables had been used in only six studies addressing the potential influences of flow regimes on riverine biota.

There is no consensus as yet as to which flow variables are most relevant in hydrological classifications or for river management purposes, for describing various attributes of flow variability (Poff *et al*. 2006a). As Clausen and Biggs (2000) observed, however, in identifying core flow variables for ecohydrological studies it is important to understand the ecological relevance of the variables, the interrelationships among them (to avoid redundancy and maximise information content), and the number of variables required to adequately express the main facets of any particular flow regime. Importantly too, there is the risk that biologically meaningful information might be masked when measures of hydrological variability are combined to form simpler hydrological indices (Puckridge *et al.* 1998).

Selection of flow indices by researchers for ecohydrological studies has been based on factors such as ease in computation or personal preference, in addition to objective criteria that include perceived ecological relevance (Olden and Poff 2003; see Section 3.2, for this study), with emphasis placed on both measures of

average conditions and characteristics of extreme events (Townsend *et al*. 1987; Poff and Ward 1989; Bragg *et al*. 2005; Mathews and Richter 2007; Monk *et al*. 2007). For instance, in studies of the ecological relevance of different flow indices, Clausen and Biggs (1997, 2000) selected flow indices that were commonly used in hydrology studies and/or expressed events expected to strongly influence the benthos on the basis of stream ecosystem theory or empirical disturbance studies. Monk *et al*. (2006, 2007) selected 201 ecologically relevant flow variables from published hydroecological studies. Growns and Marsh (2000) selected variables for an analysis of the flow regimes of southeast Australian rivers if they were shown from the literature to be a useful measure of some aspect of river hydrology, as well as deemed potentially important to stream biota based on expert judgement.

Flow indices commonly used in ecohydrological studies, with a focus on low flows

Reviews of the range of flow indices, including those reflecting low flow facets, commonly used in hydroecological analyses contrasting river flow regimes can be found in Tharme (1996, 2003), Puckridge *et al.* (1998), Smakhtin (2001), Olden and Poff (2003), Pyrce (2004) and Monk *et al.* (2006).

Several measures of overall flow variability (and predictability) are considered ecologically relevant by numerous researchers, most notably the CVs of daily, maximum and minimum flows (Jowett 1997; Haines *et al.* 1988; Poff and Ward 1989; Poff 1996; see also Section 4.5), as well as measures of general flow conditions, such as mean daily discharge (Gippel and Stewardson 1998) and median flow (Q_{50}; Caissie and El-Jabi 1995; Gippel and Stewardson 1998; Clausen and Biggs 1997; Bragg *et al.* 1999, 2005; Monk *et al.* 2006). In addition, a wide array of flow indices has been used to describe the high flow regime (see various references cited in this chapter). A similarly diverse suite of indices has been used to describe river low flows. Tharme (2003, p. 428-441, Appendix 1) provides a detailed review of the specific low flow indices applied in various countries worldwide, which is not repeated here.

Globally the Q_{95} (95^{th} flow percentile) and the annual or seasonal 7Q10 (consecutive 7-day low flow event with a 1:10 year return period) appear the most commonly used low flow indices (Tharme 2003; see also Section 1.5.3). Pyrce (2004, p. 10, Table 9) provides summaries of flow duration indices used for low flow studies, and Tharme (1996), Smakhtin (2001) and Pyrce (2004, p. 6, Table 7, and p. 8, Table 8) discuss the diverse reasons behind the use of various indices. The following are also among those low flow indices frequently encountered in the literature, and represent only a fraction of a far lengthier list applied for perennial rivers (e.g. Gustard 1979; Reiser *et al.* 1989b; Bullock *et al.* 1991; Petts *et al*. 1995, 1999; Cassie and El-Jabi 1995; Tharme 1996, 2003; Clausen and Biggs 1997; Dunbar *et al.* 1998; Gippel and Stewardson 1998; Smakhtin 2001; Pyrce 2004; Bragg *et al*. 2005; Monk *et al.* 2006, 2007): Q_{96}, Q_{90} or Q_{75} (at annual and monthly scales); Q_{min}; annual 7-d minimum flow (MAM7); the median minimum (i.e. median of annual 1-day minima over the period of record); baseflow index (BFI); and 7Q2 (i.e. the lowest mean discharge over seven consecutive days, with a 2-year recurrence interval) or 7Q20; 30-75% of the 1: 5 year low flow; 1Q10 or 30Q10; Q_{50}/Q_{90}; and so on. Low flow indices regularly used as the foundation for statistical approaches

for low flow determination in gauged catchments include the annual and 10-year 7-d minimum, 1-d minimum (median annual), Q_{90}, Q_{95}, and BFI (Agnew *et al.* 2000; Smakhtin 2001).

Several ecohydrological studies and environmental flow methodologies reliant on historical flow records have moved beyond standard classification or regionalization of flow regime types or singular use of the kinds of indices above, respectively, to multivariate statistical characterization of flow variability. For example, the indices of hydrological alteration (IHAs – Section 1.5.3), which have been applied in both contexts, quantify central tendency and dispersion across the magnitude of monthly flows; magnitude, duration and timing of annual extreme events; frequency and duration of high and low flow pulses; and rate and frequency of flow changes. A subset of these indices specifically characterizes ecologically relevant flow components (Richter *et al.* 1996; Mathews and Richter 2007, p. 7, Table 1): extreme low flows, low flows, high flow pulses, small and large floods. Low flows in each month are described by 12 mean (or median) monthly low flow statistics, while extreme low flows are defined as the 10^{th} percentile of all low flows, for which the mean or median values are calculated for magnitude, frequency, duration and timing.

In one of the earliest comprehensive studies of river flow regimes focused explicitly on their ecologically meaningful features, Poff and Ward (1989) quantitatively characterised the flow predictability and variability of 78 streams representing the range of geomorphic, physiographic and ecologic regions across the continental United States. Eleven key flow statistics (plus four basin descriptors), based on an analysis of long-term, mean daily discharge records (17-81 y), were derived as aspects of the flow regime of probable ecological significance, namely: (1) three measures of overall flow variability (mean annual CV, ANNCV; Colwell's predictability, PREDQ (or *P* in this study); and the proportion of total predictability comprised by constancy, C/P); (2) six indices reflecting flood regime; and (3) two measures of intermittency extent, reflecting the average annual number of zero-flow days and potentially ecologically significant low flow periods, where discharge approached but did not reach zero. The 11 flow indices analysed resulted in nine clusters of rivers of distinct flow regime type, and with some geographic affiliation apparent, ranging from a harsh intermittent regime type (long periods of zero flow and very low flow each year) to a series of perennial river types (only occasional zero flows days). Poff and Ward (1989) anticipated certain implications for biotic community structure on the basis of the nine types of flow disturbance regime identified, with a conceptual framework based on the positions of the river types in continuous, 3-d flow space providing a means for illustrating, *a priori*, the relative contributions of ecologically important hydrological variability to the river physical template (Section 1.4.5). They felt that in all river types examined (except 'harsh intermittent'), a significant proportion of the physical template delimiting the range of biotic interactions and responses is probably established through the interactions of some combination of overall flow variability (*P* or mean annual CV), and flood predictability and frequency. Poff (1996) expanded Poff and Ward's (1989) earlier work, classifying 806 relatively undisturbed, small to medium-sized streams (and a subset of 420 sites of longest, highest calibre daily flow records) in the continental U.S.A. into stream types, on the basis of static basin descriptors (viz. basin drainage area; MAR; daily mean

discharge, QMEAN) and ten ecologically relevant flow characteristics (Section 4.5). The ten stream types delimited were later consolidated to form six general classes, by Olden and Poff (2003).

Jowett and Duncan (1990) classified 130 New Zealand rivers into six groups on the basis of flow variability, including indices reflecting the magnitude and variation of low and high flows, using both instantaneous and historical flow data (Section 4.5; see Chapter 8 for reported links between flow attributes and biota). Biggs *et al.* (1990) characterized 144 river sites in the same country according to hydrological (as well as biological and water quality – see Chapter 8) properties, with the ultimate goal of deriving models for predicting effects of altered flow regimes on aquatic biota. They were able to demonstrate the importance of flow variability and other regime characteristics (alongside water chemistry and catchment factors), in defining river ecological character. Poff and Allan (1995) in a United States study connecting hydrological regime with the functional organisation of fish assemblages used eight unusual flow variables derived from long-term historical flow records to describe streamflow variability and predictability, as well as the frequency and predictability of low flow and high flow extremes. Variables were the daily flow CV, Colwell's *P*, baseflow stability, low flow predictability (i.e. proportion of low flow events ≥ 5 y magnitude falling in a 60-d seasonal window, with low flows defined by annual 1-d minima and 5 y an arbitrary recurrence threshold for what constituted an important low flow event), low flow-free period (i.e. maximum proportion of the year during which no low flow events occurred over the period of record), flood frequency and predictability, and spate-free period. Puckridge *et al.* (1998) selected 23 measures of flow variability considered ecologically meaningful (based on a review of fish responses to three temporal scales of flow variability - long-term patterns of flow, recent hydrological events, flow pulse features), for an analysis of hydrological regimes of 52 rivers worldwide. The multivariate analysis based on these flow measures (which included general variables, e.g. variability of all monthly flows, as well as the low flow variables: variability of minimum discharges, and percentage of all months of record with zero flow) revealed distinctive patterns of flow variability of probable biological significance, with dryland and tropical rivers at the extremes. Eleven relatively independent measures of hydrological variability were identified as central in differentiating regime types (eight of which could be associated with different aspects of fish biology).

Clausen and Biggs (2000) used a principal components analysis of 35 flow variables (see Section 4.5), derived from daily flow data for 62 New Zealand perennial rivers, to identify groups of flow variables that represented different, ecologically relevant facets of the flow regime, namely attributes of river size, overall flow variability, the volume of high flows, and the frequency of high flow events. A similar analysis for rivers of the same country (using 34 hydrological indices) showed that flood frequency variables separated out from most other indices of flow variability, while the only two low flow indices examined grouped closely (Clausen and Biggs 1997) (see Chapter 8, for ecological implications). Growns and Marsh (2000) explored the use of 333 hydrological variables comprising seven categories (viz. long-term, high flow, low flow, moving average, cessation of flow, hydrograph rise and fall, and monthly flow variables) for characterizing, in an ecologically relevant way, the flow regimes of variously regulated and unregulated

southeastern Australian rivers (107 sites). By removing highly correlated variables, they reduced the number of ecologically pertinent flow variables from 333 to 91. Flow indices were considered to be ecologically significant only if they were found to be spatially or temporally correlated with patterns in stream biota. From a vast body of 171 flow indices, Olden and Poff (2003) used principal components analysis of 420 sets of long-term flow records across the continental U.S.A. to derive a subset of flow indices that minimised multicollinearity, yet adequately characterized important attributes of the flow regime for hydroecological purposes. They presented a framework that highlights the most relevant flow indices, for different river types, for nine distinct flow-regime components to which other ecologically pertinent flow indices could be added (see Olden and Poff (2003) for specific examples of its application).

In one of few studies that have combined low flow hydrology with both water chemistry and invertebrate data, Caruso (2002) examined patterns of extreme low flow associated with a severe (1998-1999) drought, at 12 river sites across the Otago Region, South Island, New Zealand. Hydrological indices determined included mean annual flow (MAF), mean annual 7 day low flow (MALF), 7-day low flow with a 10 year return period ($Q_{7,10}$ or 7Q10), and low flow durations below $Q_{7,10}$ and MALF during the extreme low flow period. Many streams experienced discharges below MALF for periods greater than two months and discharges below $Q_{7,10}$ for at least 20 days. The majority of streams (eight of 12 sites) were subjected to the lowest or second lowest discharges ever recorded, on the basis of $Q_{7,10}$ values, with one river (Shag R.) drying up to a series of pools in some reaches. The implications of such extreme low flows for water quality and instream biota are discussed in Chapters 5 and 7, respectively.

More recently, Monk *et al*. (2006, 2007) classified 83 English and Welsh rivers, based on patterns in the magnitude and form of their long-term, average annual hydrological regimes (subsequently linking flow variability and invertebrate response; Chapter 8). Principal components analysis was used to identify the most useful subsets of flow indices for characterizing different flow regime classes, from an original set of 201 indices, with the majority of the 42 variables identified across the classes representing the magnitude of average flow conditions (24), followed by the magnitude (6) and duration (4) of low flows (Monk *et al*. 2007). Five different classes of flow magnitude (based on summary statistics for mean monthly runoff) and three of annual hydrograph shape (reflecting timing of peak flow periods) were differentiated. Regional west-east trends in flow regime magnitude (high-low) and timing (early-late peak), derived from the resultant ten regime composite classes, were identified that reflected basin controls and climatic gradients.

4.2 APPROACH AND OBJECTIVES

With the above perspective on the diversity of hydroecological approaches to low flows, a comprehensive description of the natural and especially, the low flow, features of the hydrological regimes of the rivers at the study sites was undertaken, central to the evolution of subsequent thesis chapters (Objective 1, Section 1.2; Figure 1.2). Further, the natural and experimentally manipulated extreme flows (in this context,

hereafter simply referred to as 'extreme low flows') experienced at individual sites during the study were translated into a form that enabled any biophysical responses to low flows to be assessed, as far as possible, in the context of the longer-term flow disturbance history of each site. The objectives addressed were to:

1. Describe the main features of the natural hydrological regime of each river, with specific reference to flow variability and patterns of low flows, and hence, to compare site low-flow disturbance histories.
2. Contextualise both the natural discharge fluctuations observed during the study period and the experimental flow reductions, in terms of the flow disturbance history of each site. Thus, the extent to which, for each site, the experimental flow reductions represented potentially more extreme physical disturbances than natural low flows, could be ascertained.
3. Identify indices of flow variability and low flow of potential ecological relevance for invertebrates.

The analyses on which characterization of site flow regimes was based are detailed in Section 3.2. Results are given in Sections 4.3 and 4.4, with a summary discussion in Section 4.5.

4.3 CHARACTERISTICS OF NATURAL FLOW REGIMES AT THE SITES, WITH SPECIFIC REFERENCE TO LOW FLOWS

4.3.1 Site annual, seasonal and monthly flow distributions

Mean annual runoff and overall flow patterns

Approximate MAR and runoff figures percentages for the four study sites are presented in Table 4.1 and reflect differences in catchment area (Table 2.2). Mean annual runoff is greatest for the Molenaars site, at about 137 Mm^3, followed by the Elands site. Markedly lower figures are reported for the Riviersonderend and Du Toits rivers, with the lowest figure, *c*. 42 Mm^3, observed in the latter instance. Natural runoff coefficients are similar for all four sites at 60% and above (Table 4.1). The uppermost site, the mountain stream zone of the Riviersonderend, has the highest runoff coefficient, as expected based on catchment factors, such as altitude, MAP and topography (Section 2.4).

Comparison of the normalised distribution of average total monthly volumes over the period of record (Figure 4.1) indicated that all four rivers exhibit a distinctly seasonal flow pattern, with peak flows during the winter, from June to August. Transitional flow months are April-May, when a dramatic increase in flow volume occurs with the climatic change to autumn conditions, and September-October, when there is a sharp decline in flow volume with the onset of spring. In accordance with catchment characteristics (Tables 2.2 and 2.4) and MAR figures (Table 4.1), the Molenaars River has the highest volumes of flow in all months of the year, while the Du Toits River consistently has the lowest volumes (Figure 4.1). Although the catchment area of the Riviersonderend site is marginally smaller than that of the Du Toits, winter flow volumes are higher in the former river. This difference can be attributed largely to the considerably higher runoff generated by the Riviersonderend catchment (Table 4.1). The relatively greater underestimation of peak flood events at the Du Toits site compared with the Riviersonderend is, however, doubtless a contributing factor exacerbating the difference (Section 3.2.1).

Table 4.1 Observed and naturalised mean annual runoff (MAR, Mm3) estimates and naturalised runoff coefficients for the sites (from DWAF 1994, 1997, and DRIFT FDC program outputs; Section 3.2.3). Figures for MAR are approximate and therefore represented by ranges of values. Patched observed values (or equivalent - Elands) are discussed in the text. The periods of record used for calculations are indicated in parentheses. * - by NSI.

SITE	OBSERVED MAR FROM ORIGINAL DWAF DATA (x 10^6 m^3)	OBSERVED MAR FROM PATCHED DWAF DATA (x 10^6 m^3)	*NATURALISED PATCHED EXTENDED MAR (x 10^6 m^3)	NATURALISED RUNOFF COEFFICIENT (%)
Elands (EL)	87.03-96.56 (1969-1993)	- (-)	85.4 (SD = 31.43) (1928-1988)	63
Molenaars (MO)	134.50-146.11 (1969-1993)	136.70 (1969-1993)	135.53 (1927-1993)	60
Du Toits (DU)	31.21-41.33 (1964-1991)	42.19 (1964-1991)	42.01 (1927-1993)	63
Riviersonderend (RI)	59.83-60.74 (1964-1991)	61.93 (1964-1991)	60.85 (1927-1993)	68

All sites peak sharply in flow volume to winter maxima by June or July (reaching a maximum of 28.5 Mcm, for the Molenaars site, in July), following distinct flow increases in May, with the Elands attaining peak flow volume slightly earlier in the winter than the other sites (Figure 4.1). Although variation among sites in flow volumes during the winter months are considerable (and generally reflective of river sizes), all sites have similarly low flow volumes during the dry season (Figure 4.1). The dry season characteristically extends from about November to early April, with February consistently the month of lowest flow volume (0.5-1.8 Mcm, for the Du Toits and Molenaars sites, respectively). For all sites except the Riviersonderend, January to March represents a three month window of lowest flow (hereafter referred to as the 'peak dry season') below 3 Mcm. For the Riviersonderend site, the average flow volume for December is marginally lower than that of March.

Distributions of average daily discharges

Annual (Table 4.2) and monthly (Table 4.3) summary statistics, in conjunction with box-whisker plots of monthly flow distributions (Figure 4.2), revealed the temporally dynamic, but fully perennial (no recorded incidences of zero flow) nature of the flow regime at each site. The figures in Table 4.2 were calculated from patched observed DWAF data for the Elands and Molenaars sites, and from patched, revised observed data for the other two sites (cf. Table 4.3, where the use of original observed data for the Riviersonderend and Du Toits sites resulted in minor differences in minima and maxima). In the case of the Du Toits River, and to a lesser extent the Riviersonderend River, recent data revision by DWAF produced modified historical flow records that more accurately represented the daily flow distribution, particularly for previously underestimated higher flows and flood maxima than the original data (see also Section 3.2). Where

discharges differed markedly from original values, the revised (and subsequently patched) figures are presented in parentheses in Table 4.3. Comparisons of original and revised median discharges for the Du Toits and Riviersonderend sites (Table 4.4), confirmed that flows below monthly medians (representing the upper bound to the low flow regime - Smakhtin 2001) were essentially unaltered. For the purposes of this chapter, therefore, the lower, unrevised flow minima have been used for comparative purposes (DWAF provided no rationale for alterations of minima), while cognisance of the upwardly revised maxima was taken.

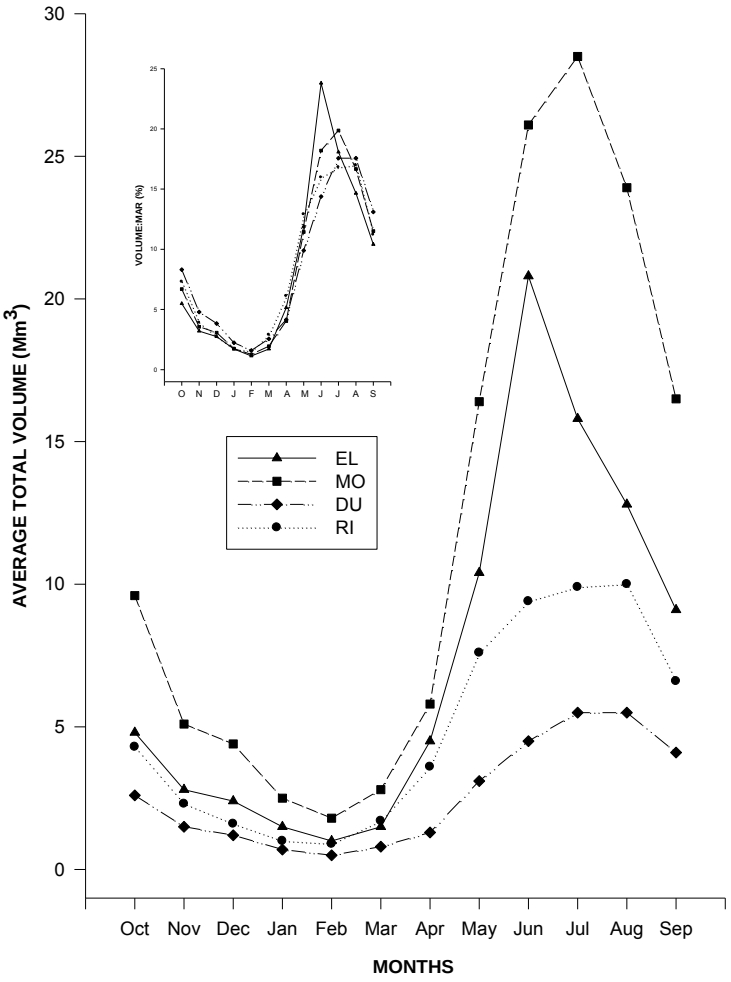


Figure 4.1 Characteristic seasonal flow patterns at the sites (expressed as average total volumes in Million m^3, Mm^3). In the inset graph, the data were normalised by MAR to eliminate scale effects due to differences in river sizes.

Overall, as envisaged on the basis of MAR and the other factors discussed above, the Molenaars site exhibits the highest Mean Annual Flow (MAF) and median discharge, followed by the similarly-sized Elands, and then the two smallest sites (Table 4.2). Calculated standard deviations around the mean, as well as minima and maxima, show that the first two rivers experience a wider range of discharges than the other sites. Minima indicate that all four sites are fully perennial. Although, according to the historical flow record, the lowest discharge of all sites occurred in the Molenaars, this is unlikely to be accurate. It is probable that the

Q_{min} for this site was more in line with the minimum ever recorded in the peak low flow month (February), 0.180 $m^3 s^{-1}$ (Table 4.3), and thus, similar to that recorded for the Elands site. Figures for Q_{max} indicated that substantially higher flood events occur at the Elands and Molenaars sites than the other two sites (Table 4.2). Unexpectedly, the highest magnitude flood was recorded for the Elands (285.500 $m^3 s^{-1}$), rather than for the parent Molenaars site. Although it is possible that flood attenuation had occurred between the two sites, it is more plausible that gauged peak flows are inaccurate (Section 3.2.1). Highest magnitude flows for the Du Toits and Riviersonderend are some 83% lower than those of the other two sites. On the basis of observed (unrevised) Q_{min} figures (Table 4.3) the relative difference in low flows is even greater than that of high flows, at roughly 98-86%.

Table 4.2 Mean (± SD), median (Q_{50}), minimum and maximum daily discharges ($m^3 s^{-1}$) over the period of historical record for each site.

SITE	PERIOD OF RECORD	NO. OF RECORDS PROCESSED	MEAN (± SD)	MEDIAN	MIN	MAX
Elands	01/04/1969-31/01/1997	10168	3.074 (± 10.134)	0.952	0.144	285.500
Molenaars	01/03/1969-31/01/1997	10199	4.601 (± 9.909)	1.602	0.001	159.100
Du Toits	01/06/1964-31/08/1992	10319	1.217 (± 2.215)	0.465	0.089	35.970
Riviersonderend	01/06/1964-31/08/1992	10319	1.973 (± 4.033)	0.567	0.058	38.580

For the Molenaars, from the monthly summary statistics presented in Table 4.3 and monthly distribution of average daily discharges depicted in Figure 4.2a, it is evident that the months of November to March represent the full extent of the dry season, with mean discharges below 2.0 $m^3 s^{-1}$, a very low range of discharges representing the 75%-95% exceedence flows, and fairly similar Q_{min} values in all months. The peak low flow months of January-March exhibit similarly low ranges in discharge, with the same median discharge in the latter two months (0.517 $m^3 s^{-1}$). The lowest range in discharge is attained in February, also when the lowest Q_{mean} (0.730 $m^3 s^{-1}$) and Q_{max} (12.320 $m^3 s^{-1}$) of all summer months were recorded. Although minima of 0.004 and 0.001 $m^3 s^{-1}$ were recorded for November and December, respectively, it is probable that Q_{min} is closer to the February figure of 0.180 $m^3 s^{-1}$. Reflecting the transition from spring to summer, high maximum discharges are experienced at the site in November and to a far lesser extent in December, while flows below 5th percentile remain well below those of April-May. Although the mean, median and lower flows in April are similar to those of peak summer, the upper range of discharges represented by the 25th-5th percentiles and Q_{max} is markedly elevated above the preceding months. This is due to the influence of fresh events and small floods with the onset of autumn. May exhibits a sharp increase in mean average daily discharge associated with the first major winter rains in the catchment. However, at the 95% exceedence level and below (see below), low flows at the end of the dry season extend into April and May, and are lower than flows representing the same percentiles in early summer (November-December). At higher flow percentiles indicative of summer freshes and early wet season floods, this trend

is no longer apparent. Mean and median discharges peak in midwinter, July. However, the widest range in discharge magnitude occurs in June (with a maximum of about 159.100 $m^3 s^{-1}$ reached). September and October represent transitional spring months.

Monthly summary statistics for the Elands site are presented in Table 4.3, while the monthly distribution of average daily discharges is given in Figure 4.2b. November to March represent the typical extent of the dry season, with mean discharge magnitudes at, or mostly below 1.0 $m^3 s^{-1}$, and a low range of discharges representing the 75%-95% exceedence flows. Highly similar Q_{min} values are experienced in the peak dry season, from January to March (0.140-0.190 $m^3 s^{-1}$). The flow range is narrowest in February, with the lowest recorded mean (0.391 $m^3 s^{-1}$) and median (0.316 $m^3 s^{-1}$) discharges of all months. High flow events in this month are of considerably lower magnitude than for values for the months either side (Q_{max} = 6.490 $m^3 s^{-1}$, versus 20.180 and 16.390 $m^3 s^{-1}$), indicating a short period of very stable low flows and few fresh events. The lower flows (as represented by the 95th percentile) experienced at the site over much of the dry season are highly similar, in the order of 0.2 $m^3 s^{-1}$, indicating a fairly constant low flow regime that may extend into April. Although the April median discharge falls below the December median flow, the mean discharge in the former month exceeds the equivalent discharges in November and December, reflecting the onset of the wet season. Typically, the range of different magnitude discharges also gradually increases from April, through May, to the wet season proper. Although the Q_{50} is highest in July, the timing of the peak magnitude floods of the winter is typically June, when the range (and mean) of high flows is greatest. September and October (spring) are transitional months in terms of the overall distribution of flows.

Monthly summary statistics and the distribution of average daily discharges for the Du Toits site are provided in Table 4.3 and Figure 4.2c, respectively. At this site, the range of discharges over the summer is fairly wide, especially in the upper 25th-5th percentiles. The peak of the dry season is delimited by the months January to March, all of which exhibit average and median discharges less than 0.6 $m^3 s^{-1}$ and 0.2 $m^3 s^{-1}$, respectively. Although the March median is marginally lower than that of February, the upper range of flows occurring in the river in the former month is broader. The narrowest range of flows occurs in February, which represents a period of stable low flow. Mean and maximum monthly discharges were also lowest overall in this month, at 0.225 and 4.257 $m^3 s^{-1}$, respectively. According to the historical record, however, the lowest flow on record occurred in January, a mere 0.003 $m^3 s^{-1}$ and the lowest discharge across all sites (Table 4.2 cf. Table 4.3). Monthly minima of similar magnitude, in the order of 0.1 $m^3 s^{-1}$, occurred over the remainder of summer. Mean and maximum discharges increase markedly from April to May with the shift to autumn. Revised monthly maxima (Section 3.2.1) indicate that the winter period is characterised by similar peak flows (5th percentile flows and above) from June to August. Although Q_{max} is reached in June (35.970 $m^3 s^{-1}$), marginally higher mean and median flows are documented for July and, to a lesser extent, August. Mean average daily discharge tails off progressively from late spring into the dry season, but the wide range in higher flows (Q_5 to Q_{max}) is retained.

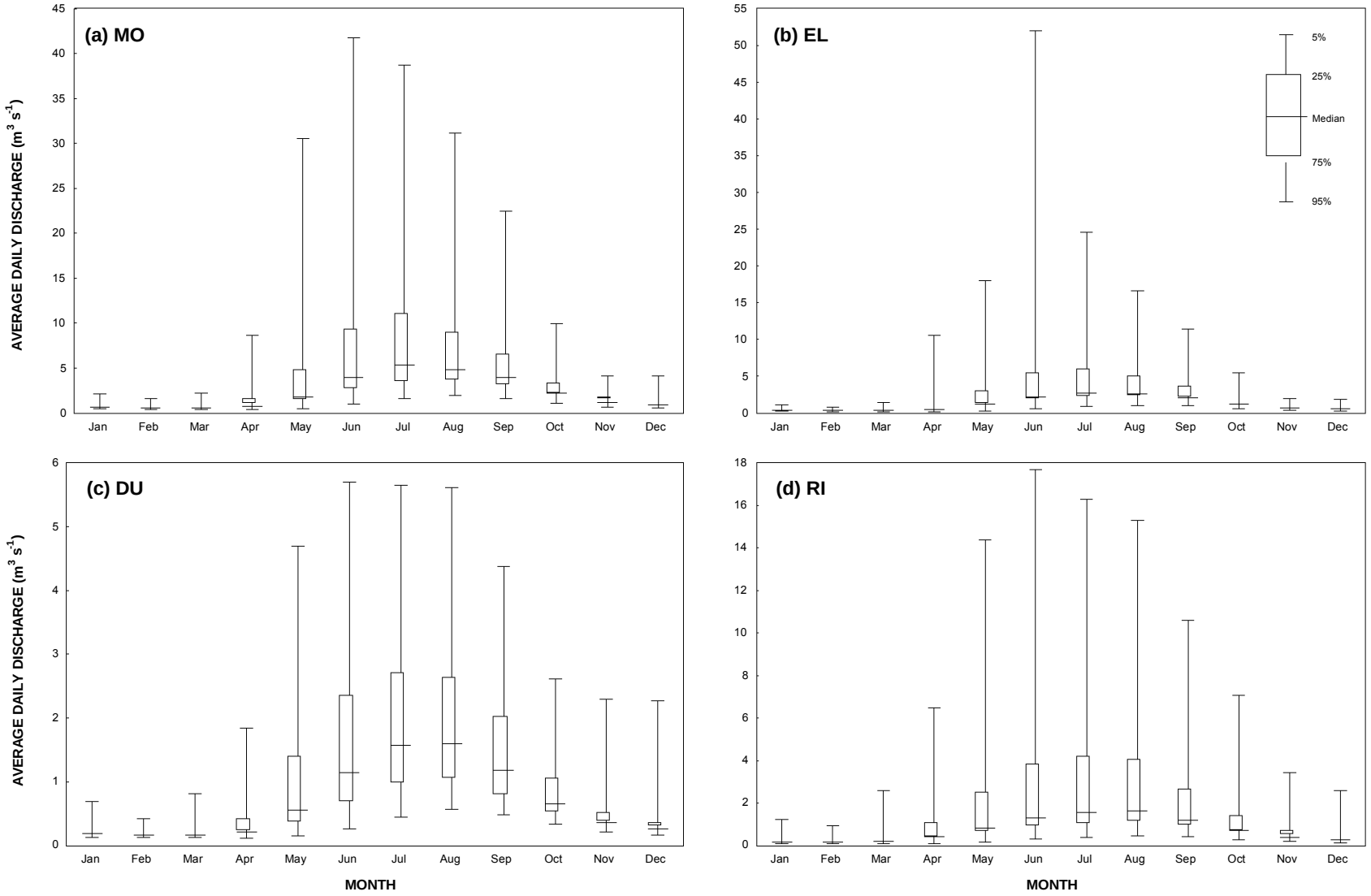


Figure 4.2 Monthly distribution of average daily discharges ($m^3 s^{-1}$) at the (a) Molenaars, (b) Elands, (c) Du Toits, and (d) Riviersonderend sites. The various percentiles indicated are for the full period of observed (non-patched record). *For DU and RI the upper bounds of the discharge distributions are underestimated, particularly from Jun-Aug.

Table 4.3 **Mean, minimum and maximum average daily discharges ($m^3 s^{-1}$) by month for each site.** Where different from the original data, revised patched figures are presented in parentheses.

SITE	ELANDS (03/1969-02/1997)			MOLENAARS (02/1969-01/1997)			DU TOITS (10/1964-08/1992)			RIVIERSONDERED (10/1964-06/1992)		
	Mean	Min	Max	Mean	Min	Max	Mean[c]	Min	Max[c]	Mean[d]	Min	Max[d]
JAN	0.545	0.190	20.810	0.920	0.330	26.240	0.252 (0.323)	0.003 (0.089)	5.030 (18.560)	0.388 (0.409)	0.073	20.500 (25.490)
FEB	0.391	0.140	6.490	0.730	0.180	12.320	0.225	0.120	3.650 (4.257)	0.350	0.020 (0.083)	12.700 (12.650)
MAR	0.578	0.140	16.390	1.040	0.280	33.610	0.304 (0.316)	0.109	5.660 (9.192)	0.632	0.050 (0.083)	18.000 (20.020)
APR	1.743	0.180	37.310	2.230	0.250	57.370	0.487 (0.562)	0.101	5.830 (10.600)	1.392 (1.379)	0.093	19.500 (22.070)
MAY	3.866	0.210	58.240	6.110	0.340	90.780	1.175 (1.477)	0.122	6.100 (26.030)	2.842 (2.958)	0.098	28.900 (34.690)
JUN	8.021	0.360	280.600[a]	10.080	0.560	159.100	1.744 (2.477)	0.159	6.100 (35.970)	3.644 (4.033)	0.169	29.900 (36.870)
JUL	5.881	0.400	64.360	10.650	0.610	157.500	2.051 (2.598)	0.170	6.100 (26.980)	3.695 (3.988)	0.162	31.300 (38.580)
AUG	4.775	0.610	61.330	8.920	1.090	96.950	2.069 (2.579)	0.324	6.100 (31.730)	3.721 (3.783)	0.290 (0.308)	28.800 (34.950)
SEP	3.515	0.740	39.070	6.380	1.310	58.900	1.585 (1.708)	0.376	6.100 (14.380)	2.565 (2.619)	0.320	23.400 (23.910)
OCT	1.809	0.450	35.040	3.580	0.840	62.450	0.964 (1.033)	0.269	6.090 (10.940)	1.607 (1.601)	0.202	25.000 (26.080)
NOV	1.067	0.300	79.640	1.980	0.004[b]	106.200	0.573 (0.610)	0.166	6.070 (18.670)	0.892	0.144	25.300 (30.270)
DEC	0.885	0.270	24.260	1.630	0.001[b]	42.510	0.449 (0.467)	0.140	5.380 (7.692)	0.606 (0.688)	0.058	15.900 (20.120)

[a] Comparison of Elands and Molenaars flow records for the period over which this flood event occurred shown no concordance, suggesting that this figure may be an unreliable overestimate.

[b] On the basis of the size and overall flow character of the Molenaars, it is unlikely that such low minima were recorded in either month.

[c] For the Du Toits site, monthly average and particularly, maximum discharges, were markedly underestimated in the original DWAF data set for all months.

[d] For the Riviersonderend site, maxima and hence, mean monthly discharges, were somewhat underestimated in the original DWAF data set for all months.

For the Riviersonderend site, monthly summary statistics are provided in Table 4.3, while the monthly distribution of average daily discharges is illustrated in Figure 4.2d. On the basis of median discharges, November to March represents the typical extent of the dry season. The lowest flow range occurs in February, which exhibited the lowest minimum (0.020 m^3 s^{-1}) and mean (0.350 m^3 s^{-1}) discharge of all months, as well as the smallest Q_{max} (12.650 m^3 s^{-1}) over the peak dry season. Median discharge figures are similarly low for January and February (0.172 and 0.174 m^3 s^{-1}), increasing marginally in March. Outside of the peak dry season, elevated flows represented by the 25th and lower percentiles, indicate an increasing influence of freshes and small floods on the flow regime in both autumn and spring. The river at the site exhibits a fairly early and rapid response in hydrological regime to winter flow conditions, with some relatively high flow events occurring in May. Revised monthly discharge data for winter, June-August indicate that the original observed distribution of flows, as illustrated in Figure 4.2d, was skewed by an underestimation of flood events (Section 3.2.1). The revised figures presented in Table 4.3 indicate that although the overall maximum discharge was attained in July, the mean flow was greatest in June.

Cross-site comparison of the distribution of average daily discharges (Table 4.3 and Figure 4.2) revealed similarities in the seasonal pattern of discharges, reflecting the distributions of flow volumes (Figure 4.1). February was found to be the most stable and consistent month in terms of low flows, while similarly low ranges in discharge were observed for the adjoining dry season months of January and March. Although the majority of flows remained low in these latter months, markedly elevated discharges (as a result of fresh events) were shown to occur. Marked increases in discharge were associated with both the commencement and end of summer. Such increases in flow appeared most pronounced for the Riviersonderend and Du Toits rivers, in November and December (Figure 4.2). Lesser consistency than for the dry season was found in the month of highest flows during winter, particularly when comparing the Elands with the other sites.

Table 4.4 **Comparison of median discharge figures (m^3 s^{-1}) calculated from (1) original observed historical flow records and (2) revised, patched records for the Du Toits and Riviersonderend sites.** Revised medians are given only for months where figures differ from the original data (Section 3.2.1).

STUDY MONTH	DU TOITS (10/1964-08/1992)		RIVIERSONDERED (10/1964-06/1992)	
	(1) Original Median	(2) Revised Median	(1) Original Median	(2) Revised Median
JAN	0.191		0.172	0.177
FEB	0.171		0.174	
MAR	0.166		0.195	0.204
APR	0.214	0.224	0.419	0.394
MAY	0.556	0.577	0.836	0.823
DEC	0.267		0.251	0.269
OVERALL	0.440	0.465	0.560	0.567

4.3.2 Comparative assessment of flow regime variability across sites

Various indices of hydrological variability calculated for each of the sites, over a range of temporal scales, are presented in Table 4.5 (and described in Section 3.2.3). Although it was not possible to use fully coincident periods of historical flow record, overlapping records of the same length were used.

Emphasis was placed on annual CV as the most commonly reported index of flow variability (Sections 4.1 and 4.5). The Elands site was shown to have the highest overall variability in flow regime (CV = 330%) and the Du Toits site the lowest variability, at 182% (Table 4.5). Similar intermediate levels of variability were recorded for the other sites. Intra-site comparison of monthly CVs (based on flow volumes) showed a tendency for lowest monthly variability to occur in July, August or September (Table 4.5). For all sites, except the Riviersonderend, February monthly CVs were second lowest across all months of the year. Maximum monthly CVs occurred in March for all sites, except the Elands where variability peaked slightly later. Comparison of monthly CVs among sites indicated a tendency for maximum variability for the Elands from late summer, through much of the wet season, into spring. The Molenaars site consistently exhibited intermediate levels of variability, while the Riviersondered site showed lowest or intermediate monthly variability, except in February.

February CVs were consistently lower than those of the peak dry season (Dry period CV) (Table 4.5). The highest flow variability in February and the peak dry season were recorded for the Riviersonderend, at 230% and 280%, respectively. Least variability in February was recorded for the Du Toits site (CV = 96%). Based on the three lowest-flow months, however, a marginally lower CV, 195%, was recorded for the Molenaars than the Du Toits site. In both instances, February CVs calculated using flow volumes exhibited the same trend (Table 4.5). Coefficients of variation describing the variability in lowest recorded discharges (Q_{min}) and in recorded 7-day minimum flows (Q7d-low) were found to be highest for the Elands site, at 158% and 262%, respectively (Table 4.5). Lowest variability in 1-day minima was recorded for the Riviersonderend (CV = 65%), and for the Molenaars for the 7-day consecutive low flow. The CVs for Q_{min} values were consistently lower than those of the Q7d-low flows. In all months, excluding December, lowest values of the $S_{\log x}$ index of variability, based on the slope of monthly FDCs (Section 3.2.3), were obtained for the Du Toits site (Table 4.5). Maxima were less consistent across months, with the Molenaars exhibiting the highest values of the index in four of the six study months, including the low flow months of January and February (Table 4.5).

The highest and lowest annual I_v values, an index of the year-to-year variability of peak floods and hence, flashiness of high flows, were determined for the Riviersonderend and Du Toits sites respectively. The former site also showed the highest monthly I_v figures from December to March, while the Elands reach had consistently the highest values from April to July. Far less consistency in results was obtained for the monthly index of variation in higher flows, I_v, than for monthly CVs (Table 4.5).

Table 4.5 **Indices of hydrological variability for the sites.** CV = coefficient of variation; I_V = index of variation of high flows. Low flow CVs over the period Jan-Mar (Dry period CV) and for the lowest flow month, February (Feb CV), also are provided. All indices were calculated from average daily discharges (m^3 s^{-1}) except monthly CVs (obtained from monthly flow volumes, Mcm). For individual indices, across the sites, maxima are highlighted in bold and minima in italics.

INDEX	ELANDS	MOLENAARS	DU TOITS	RIVIERSONDEREND
Period of record (No. of years)	01/04/1969-31/01/1997 (27)	01/03/1969-31/01/1997 (27)	01/06/1964-31/08/1992 (27)	01/06/1964-31/08/1992 (27)
Annual CV	**3.297**	2.154	*1.820*	2.044
Annual I_V	0.521	0.524	*0.493*	**0.575**
Monthly CV				
Jan	*0.740*	0.762	**1.086**	0.902
Feb	0.479	0.509	*0.470*	**0.680**
Mar	**1.353**	1.147	1.135	*1.000*
Apr	**1.734**	0.934	0.728	*0.692*
May	**0.882**	0.681	0.648	*0.542*
Jun	**1.613**	0.703	*0.547*	0.548
Jul	**0.770**	0.537	0.439	*0.400*
Aug	0.461	0.444	**0.517**	*0.411*
Sep	**0.557**	0.550	0.487	*0.400*
Oct	**0.637**	0.633	*0.567*	0.597
Nov	**0.928**	0.893	0.888	*0.790*
Dec	*0.849*	0.896	**1.075**	0.914
Monthly I_V				
Jan	*0.219*	*0.219*	0.267	**0.299**
Feb	0.184	0.189	*0.172*	**0.281**
Mar	0.340	*0.285*	0.299	**0.362**
Apr	**0.460**	0.402	*0.350*	0.413
May	**0.384**	0.381	0.350	*0.275*
Jun	**0.479**	0.367	0.322	*0.276*
Jul	**0.318**	0.290	0.256	*0.198*
Aug	0.175	0.172	**0.179**	*0.158*
Sep	0.235	**0.244**	0.225	*0.186*
Oct	0.257	0.257	*0.237*	**0.287**
Nov	0.264	**0.268**	*0.260*	0.261
Dec	*0.267*	0.285	0.280	**0.356**
Monthly $s_{\log x}$				
Jan	0.075	**0.106**	*0.035*	0.091
Feb	0.049	**0.090**	*0.031*	0.075
Mar	0.074	0.114	*0.067*	**0.155**
Apr	**0.296**	0.259	*0.122*	0.254
May	0.356	**0.407**	*0.211*	0.343
Dec	*0.105*	**0.158**	0.136	0.134
Dry period CV	2.290	*1.954*	2.179	**2.797**
Feb CV	0.966	1.086	*0.964*	**2.295**
Q_{min} CV	**1.580**	0.725	0.866	*0.647*
Q7d-low CV	**2.621**	*0.842*	0.947	0.960

The hydrological variability of flow regimes has been contrasted with regime predictability using Colwell's indices (Section 3.2.3). Indices of predictability (*P*), and the component indices, constancy (*C*) and contingency (*M*) are presented in Table 4.6, for both a standard examination of the entire flow regime (a) and one focused on low flows (b); corresponding state matrices are provided in Appendix 4.2.

Perhaps surprisingly, general predictability was highest for the Elands site (Table 4.6a), at 0.49, the site for which annual flow variability (CV) was greatest. This result may be attributable to the very narrow overall range in *P* values, from 0.4-0.5. Indeed, all site values, except that of the Riviersonderend, essentially round to the same figure (Table 4.6a). Predictability was lowest for the Riviersonderend flow regime ($P = 0.43$), which showed the highest CVs for February and the peak dry season. Predictability was primarily a function of low levels of flow constancy among months.

Table 4.6 Indices of hydrological predictability (*P*), and component indices constancy (*C*) and contingency (*M*), for the sites. The indices were generated from Colwell analyses using (a) a series of standard monthly flow classes ($n = 7$) and (b) a series of monthly, low flow-focused classes ($n = 15$). For individual indices across the sites maxima are in bold and minima in italics.

COLWELL ANALYSES	NO. OF YEARS OF RECORD	*P*	*C*	*M*
(a) STANDARD				
Elands	27	**0.49**	**0.25**	*0.24*
Molenaars	27	0.47	0.21	0.26
Du Toits	27	0.46	0.19	**0.27**
Riviersonderend	27	*0.43*	*0.16*	**0.27**
(b) LOW FLOW				
Elands	27	0.40	0.12	**0.28**
Molenaars	27	**0.42**	0.14	**0.28**
Du Toits	27	**0.42**	**0.15**	*0.27*
Riviersonderend	27	*0.37*	*0.10*	*0.27*

A second analysis focused specifically on the low flow regime yielded a similarly narrow range of *P* values (Table 4.6b). A marginal shift in maximum predictability away from the Elands was observed, with all sites except the Riviersonderend exhibiting *P* values around 0.4. In all cases, predictability was conferred primarily by high contingency, while constancy indices were again low. As found for the overall flow regime, the low flow regime of the Riviersonderend was the least predictable of all, a result which corresponded well with the high flow variability at this site during the dry season.

4.3.3 Comparisons of flow percentiles at annual and monthly scales, with particular focus on the low flow regime

Annual and February FDCs (monthly FDCs for other months are not depicted, but follow the same form) for the sites are illustrated in Figures 4.3 and 4.4, respectively. The full suite of percentiles (Q_1-Q_{99}) estimated from FDCs for the study period is provided for all sites in Appendix 4.1, at annual and monthly scales. It included all standard low flow percentiles above the median discharge: Q_{75} (only for monthly FDCs); Q_{80}; Q_{90}; Q_{95}; and Q_{99}. The same range of percentiles was also determined from FDCs spanning the peak of the dry season, from January to March inclusive (Appendix 4.1).

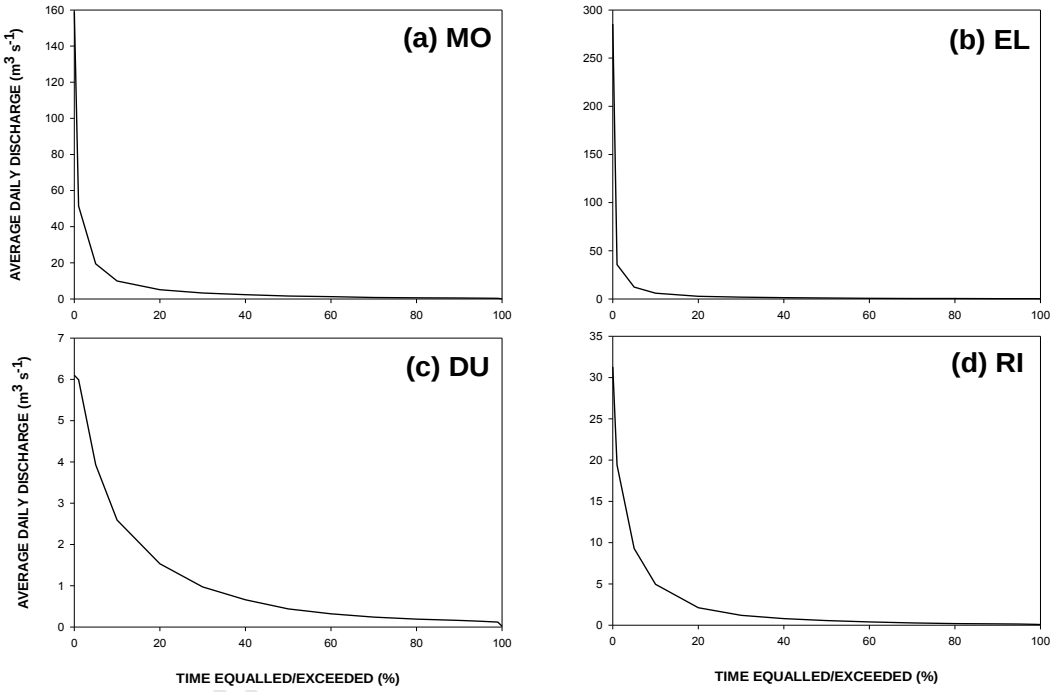


Figure 4.3 Annual flow duration curves (FDCs) for the sites. (a) MO = Molenaars, (b) EL = Elands, (c) DU - Du Toits and (d) RI = Riviersonderend. The upper portions of the FDCs for DU, and to a lesser extent RI, are truncated, particularly for exceedences below Q_{50}, due to the underestimation of floods.

The annual FDC for the Molenaars (Figure 4.3a), follows a characteristic natural shape, with a sharp decrease from discharges representing percentage exceedence values for high flows (Q_5 = 19.410 m^3 s^{-1}) to a Q_{50} of about 1.640 m^3 s^{-1}. At the low flow end of the FDC, discharges corresponding to Q_{90} and Q_{95} percentile flows were found to be highly similar at 0.480 m^3 s^{-1} and 0.440 m^3 s^{-1}, respectively, with greater differences in discharge associated with other low flow percentiles (Appendix 4.1). A similarly shaped annual FDC was obtained for the Elands (Figure 4.3b), with a distinct decrease from a high Q_5 of 12.190 m^3 s^{-1} to only 0.930 m^3 s^{-1} as a median discharge. The lower end of the FDC was extended over a narrow range

in discharges from a Q_{90} of 0.280 $m^3 s^{-1}$ to a Q_{99} of 0.200 $m^3 s^{-1}$ (Appendix 4.1). The characteristic shape of the Du Toits annual FDC (Figure 4.3c) was artificially altered by the truncation of the upper range of flows at just above 6 $m^3 s^{-1}$. Inclusion of the revised high flow figures would have produced a curve more closely resembling that of the Riviersonderend (Figure 4.3d), as the two sites share similar high flow characteristics (Table 4.3). The lower end of the Du Toits FDC flattens out from Q_{50} (0.440 $m^3 s^{-1}$), with small differences in the values of the Q_{70}-Q_{99} percentiles (0.240-0.120 $m^3 s^{-1}$, respectively) (Figure 4.3c and Appendix 4.1). The lower range of the annual FDC for the Riviersonderend (Figure 4.3d) is marginally less extended than that of the Du Toits, with similarly low flows representing the Q_{80}-Q_{99} percentiles (0.200-0.100 $m^3 s^{-1}$, respectively). The upper bound of the low flow regime is represented by a Q_{50} of 0.560 $m^3 s^{-1}$, above which Q_5 provides an indication of the upper high flow component of the annual curve (9.300 $m^3 s^{-1}$).

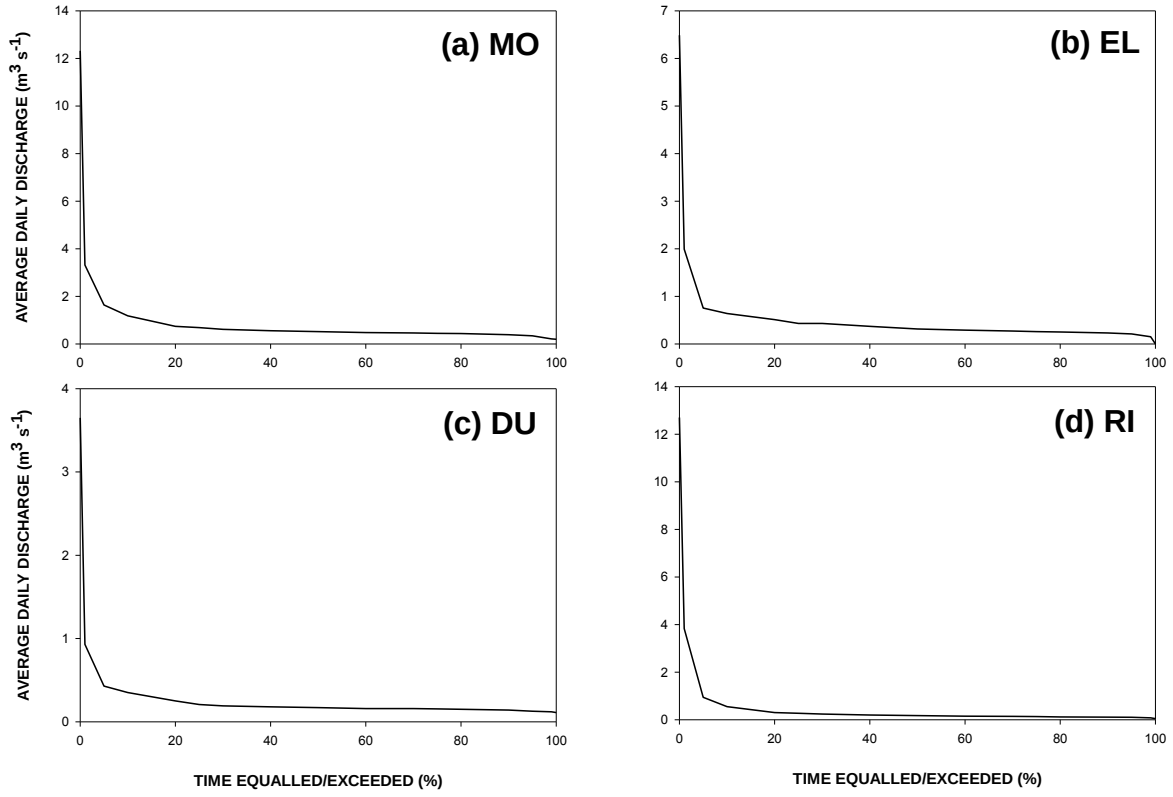


Figure 4.4 Monthly FDCs for the peak low flow month of February, for the sites.

As with the annual FDCs, general patterns for the one-month FDCs derived for the lowest flow month of February were highly similar among sites, while also retaining the differences in river size apparent from preceding results. Discharges corresponding to the main flow percentiles identified for each February curve are presented in Appendix 4.1. Differences in the discharges represented by the February low flow percentiles for the Elands (Figure 4.4b), Du Toits (Figure 4.4c) and Riviersonderend (Figure 4.4d) were similarly small for the Q_{50}-Q_{99} indices. The lowest Q_{95} value overall was obtained for the Riviersonderend

site at 0.097 $m^3 s^{-1}$, followed closely by the Du Toits River (Appendix 4.1). The greatest divergence between low flow percentiles, for the Molenaars February FDC (Figure 4.4a), probably is a function of the greater magnitude flows experienced at this site (e.g. February Q_{mean} = 0.730 $m^3 s^{-1}$, contrasted with relatively lower mean flows at the other sites - Table 4.3). Median flow percentiles ranged from 0.517 $m^3 s^{-1}$, for the Molenaars site, to 0.171 $m^3 s^{-1}$, at the Du Toits site (marginally lower than the Riviersonderend Q_{50}) (Appendix 4.1).

Normalisation of annual low flow percentiles by annual Q_{50} ($m^3 s^{-1}$) enabled direct comparison among sites (Table 4.7). Normalised percentiles closer to a value of 1 indicate close agreement with the median discharge, while lower figures reflect greater divergence from this upper bound to the low flow regime. For all low flow percentiles examined, the Du Toits site showed the greatest agreement with Q_{50}, and the Riviersonderend consistently the lowest match (Table 4.7). As expected, of all indices, greatest divergence from the 50th percentile was found for Q_{99} and lowest for Q_{80} (Table 4.7). Flow proportions representing the Q_{90} and Q_{95} indices typically were most similar.

Further comparison of low flow indices for the sites was possible using normalised percentiles for the three-month period representing the peak of the dry season (Table 4.7 and Appendix 4.1). Similar within-site trends among low flow indices were in evidence, with the Q_{99} markedly divergent from the median flow. Again, the Du Toits site exhibited the least difference between Q_{50} values and those for the standard low flow indices, while the Riviersonderend showed the greatest divergence. For Q_{99}, the latter site and the Molenaars were both at 50% of the Q_{50}. As envisaged, there was a far greater departure from median figures for annual than dry-season low flow percentiles (Table 4.7), due to the influence of high flow events in the former instance.

Table 4.7 **Comparison of standard low flow percentiles derived from annual and dry-period (January-March) flow duration curves (FDCs) for the sites.** Percentiles were normalised by the median of the annual or dry-period daily discharge, respectively, for inter-site comparisons; where appropriate, revised median flows (Table 4.4) were used.

FLOW PERCENTILES	ELANDS	MOLENAARS	DU TOITS	RIVIERSONDEREND
Annual				
Q_{80}	0.409	0.372	0.409	0.353
Q_{90}	0.301	0.293	0.344	0.265
Q_{95}	0.269	0.268	0.301	0.229
Q_{99}	0.215	0.201	0.258	0.176
Dry period				
Q_{80}	0.743	0.821	0.833	0.722
Q_{90}	0.686	0.750	0.778	0.667
Q_{95}	0.629	0.679	0.722	0.611
Q_{99}	0.457	0.500	0.667	0.500

The above comparison of percentiles was extended to examine the relationships among normalised low flow indices for individual months, within and among sites (Figure 4.5). Normalisation of Q_{90} generated a common index of baseflow contribution (Section 3.2.3). Different trends in the relative proportions of median flow represented by the various low flow indices were evident for each site (Figure 4.5a-d). Typically, for December and the consecutive peak months of the dry season, however, all low flow indices except Q_{99} were above 0.5, a figure representing a discharge threshold of exactly half that of the median monthly discharge (a value of 1 would represent 100% correspondence with Q_{50}). Percentiles all diverged most from this relationship in the months of April and May, due to the increased influence of higher flows on the medians, while the lowest flows remain disproportionately depressed. Across all sites, very little difference was observed between Q_{75} and Q_{80} indices, and similarly between Q_{90} and Q_{95} indices. Convergence for the two sets of indices during the driest months was greatest for the former pair, occurring in any one of the three months representing the peak dry season. In the Elands (Figure 4.5a) low flow percentiles appeared to be most similar to one another in January and to a slightly lesser extent in April, with the converse situation found for the Riviersonderend (Figure 4.5d). Greatest convergence of indices occurred in December for the Molenaars (Figure 4.5b), and in March in the case of the Du Toits River (Figure 4.5c). All low flow indices except Q_{99} observed the same general pattern. The latter index was shown to be by far the least consistent measure overall, especially for the months of December-March, doubtless as a result of the influence exerted on it by extreme events (outliers). The month(s) in which this index differed most from the other indices also was inconsistent, ranging from December in the Riviersonderend (Figure 4.5d) through to February-March for the Elands site (Figure 4.5a).

4.3.4 Comparison of time series of minimum flows across sites and correspondence with low flow exceedence values

Extreme low events, such as the 1-day minimum discharge in a specific month (or the minimum flow for other temporal windows), for each year of record, or the absolute minimum ever recorded in that month, assume particular importance in any attempt to understand a river's characteristic low flow regime. Time series of the natural fluctuations in 1-day minimum monthly discharges over the historical record at each site are presented in Figures 4.6a-d. Specific minima for the lowest flow month, February, are highlighted, and the long-term median monthly discharge for February is plotted as a reference. Time series of minimum consecutive 7-day low flows (Q7d-low) in each month yielded highly similar results (although discharges were marginally elevated above 1-day minima), and are therefore not illustrated.

Several trends in the low flow time series common to all four sites are apparent (Figure 4.6). Firstly, although a measure of lowest flows on record, there remains considerable variability in minima over time. This variation is strongly seasonal, with far greater amplitude in Q_{min} values outside the more stable, peak dry season. February minima are typically the lowest of all months and tend to be stable across the record. They are affected by higher flows in wet years, however, as shown by occasional values above the long-term

February median. Extreme low flow events occur infrequently (by definition), usually with only one or two events recorded over a complete 27-year record (Figure 4.6).

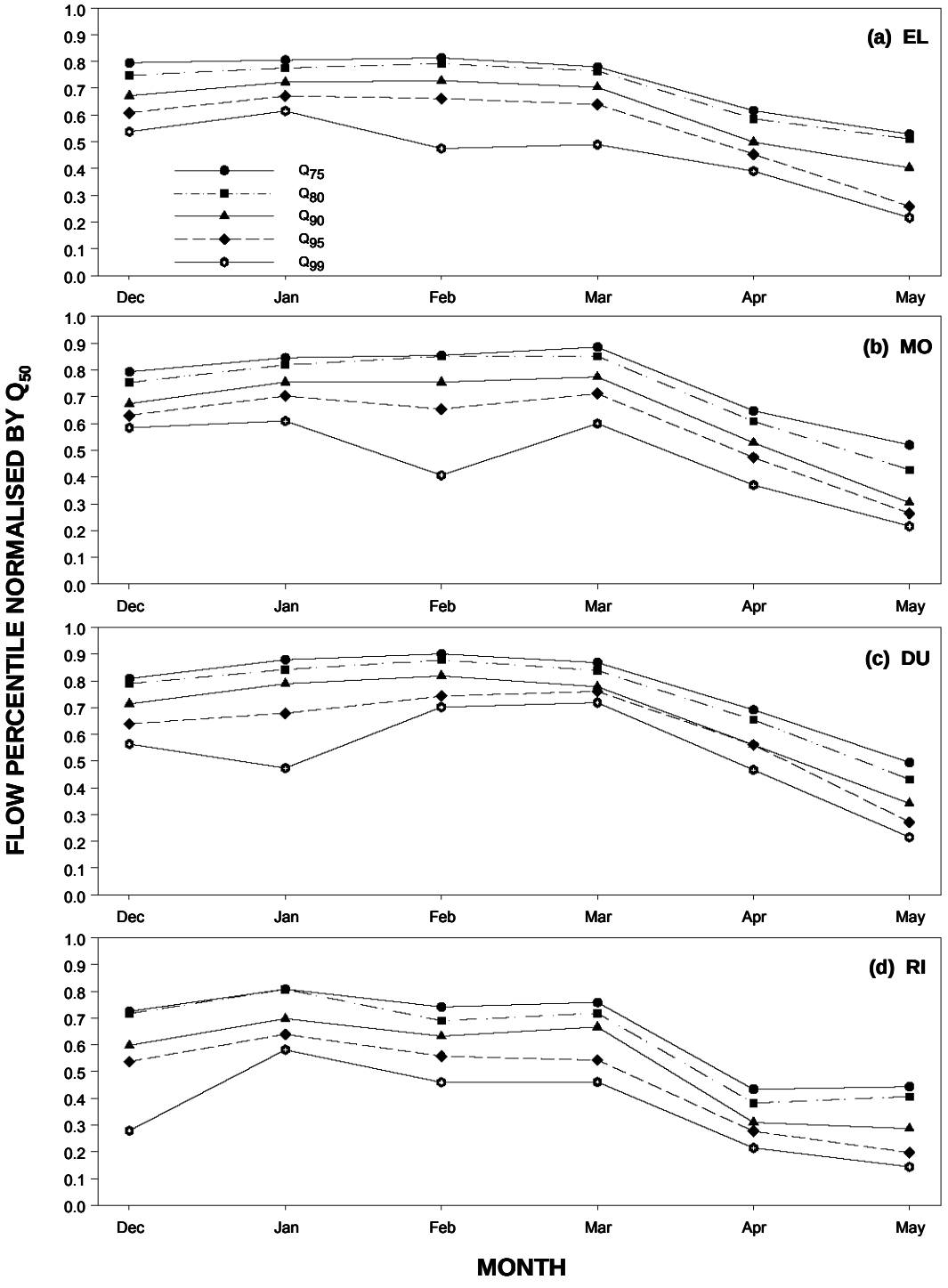


Figure 4.5 Trends in low-flow percentiles Q_{75}-Q_{99}, derived from monthly FDCs, over the study period at each site. Percentiles are normalised by monthly median discharges to facilitate inter-site comparisons. (a) EL = Elands, (b) MO = Molenaars, (c) DU = Du Toits and (d) RI = Riviersonderend.

In the case of the Elands site (Figure 4.6a) the distribution of natural minima tended to be consistent over time, falling below the long-term February Q_{50} but seldom being extremely low. However, variability in minima was pronounced during the winter months. Among years, elevated dry season minima were evident during the wetter periods of record. A fairly similar pattern was observed for the minimum flow time series for the Molenaars site (Figure 4.6b), although inter-annual variability in minima was reduced. Although a few occasions of extreme low flow were recorded, this might be a function of poor record accuracy at low flows (Table 4.3). At the Du Toits and Riviersonderend sites (Figures 4.6c and 4.6d, respectively), flows reached very low levels more frequently than at the other two sites. The minimum time series for the Du Toits clearly showed that during the dry season, and particularly in February, the lowest flows occupy a narrow range just below the long-term median discharge (Figure 4.6c). This 'compression' of the low flow regime conferred dry season stability. Very few incidences of minima exceeding the February Q_{50} were observed, suggesting a lesser influence of wet years than for the Elands and Molenaars rivers. A single near-zero low flow was apparent in the record, representing the absolute Q_{min} (0.003 $m^3 s^{-1}$, January 1988 - Table 4.3). The pattern of flow minima at the Riviersonderend site was less regular than for the other sites, with a wide amplitude in February minima below the long-term upper bound of the low flow regime in that month (Q_{50}) (Figure 4.6d); there was only one instance of a February minimum discharge exceeding the long-term median flow. The apparent lower temporal stability of the lower end of the flow regime was supported by the low predictability indices and high variability indices determined for the Riviersonderend over the dry season (see above). There was solely one instance, however, where flow dropped close to zero, at 0.020 $m^3 s^{-1}$ in February 1965 (Table 4.3).

The flow percentiles corresponding with the absolute minimum flows recorded in each month (Q Min Min), over the entire historical flow record, are given in Table 4.8, for each of the study months. Clearly, the absolute minima are extreme events in the hydrological regime for all sites (>Q_{99} for every month). Matching of the median of the 7-day low flows calculated for each month, with flow percentiles, revealed several interesting trends (Table 4.8). For individual sites, the range in percentiles representing the Q7d-low varied to different degrees across the study months. The widest range in percentiles was found for the Elands, from about 60%-87%, followed by the Du Toits site. Far narrower ranges in percentiles were found for the other sites. Comparison of percentiles for a particular month across sites revealed that 7-day low flows in the Riviersonderend River are equalled/exceeded more often in all months than at the other sites (except in May; Table 4.8). That is, the Q7d-low tends to be a lower flow at this site. For all sites, the lowest percentile Q7d-low flows tended to occur late summer (March). Maximum percentile values, in contrast, were recorded in May at all sites except the Riviersonderend (December). This can be attributed to the influence of higher flows on the shape of the monthly FDC, with low flows equalled or exceeded more frequently early and late in the dry season.

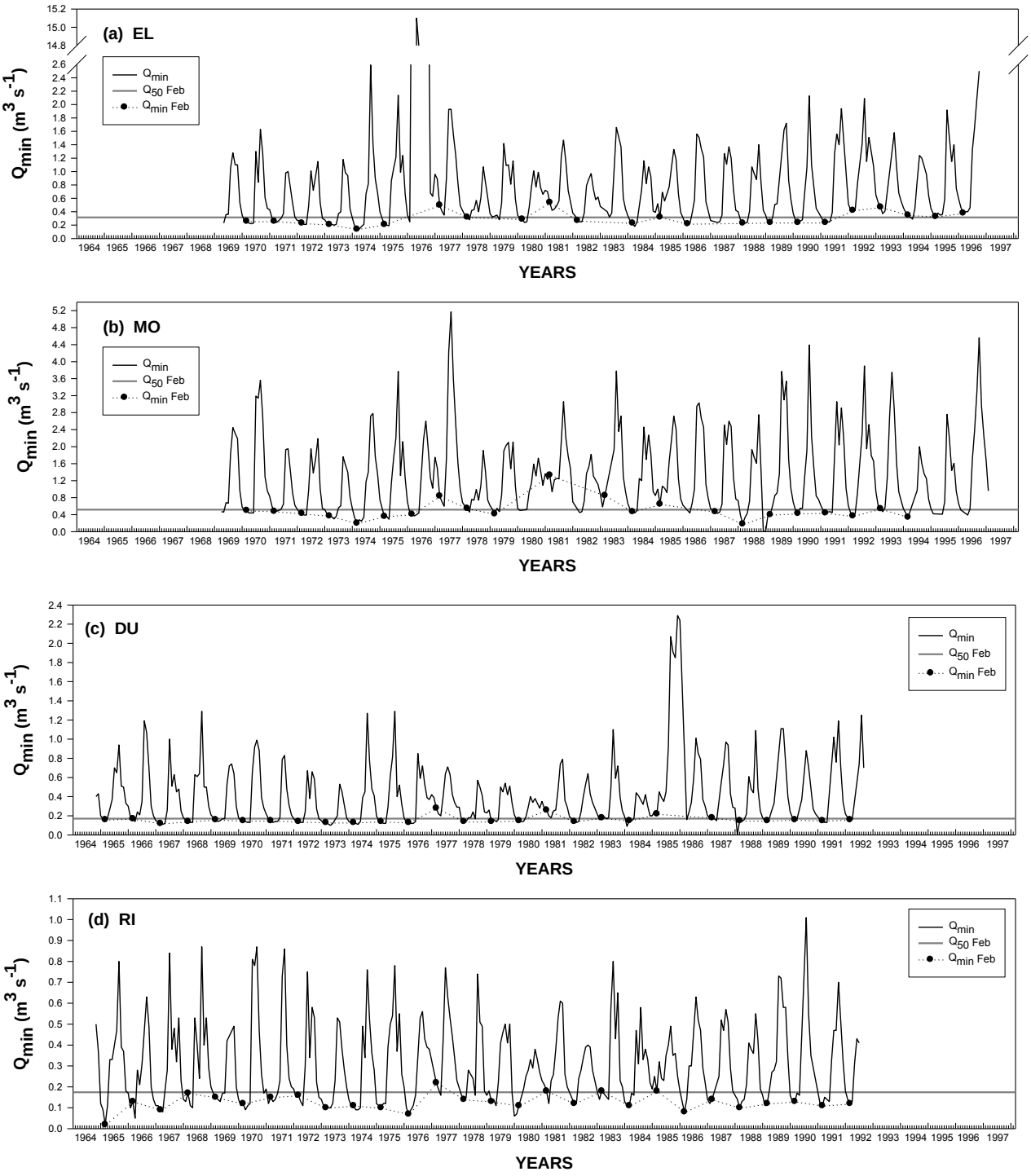


Figure 4.6 **Time series of monthly minimum discharges over the period of historical record for the (a) Elands, (b) Molenaars, (c) Du Toits, and (d) Riviersonderend sites.** February minima are highlighted, and a reference line representing the long-term February Q_{50} is shown. Occasional missing data were interpolated. A break is shown for the Elands site, for elevated minima during 1976.

Table 4.8 Flow percentiles corresponding with the natural, absolute minimum discharge (Q Min Min; $m^3 s^{-1}$) and median seven-day low flow for each month of the study period (Q Median 7d-low; $m^3 s^{-1}$), for each site. Percentiles were calculated from monthly FDCs (Appendix 4.1).

LOW FLOW INDEX MONTH	FLOW PERCENTILE			
	Elands	Molenaars	Du Toits	Riviersonderend
Q Min Min				
Dec	99.9	99.9	99.9	99.9
Jan	99.9	99.9	99.9	99.8
Feb	99.8	99.8	99.9	99.9
Mar	99.9	99.9	99.9	99.9
Apr	99.8	99.9	99.8	99.9
May	99.9	99.9	99.9	99.9
Q Median 7d-low				
Dec	72.3	74.1	71.8	81.7
Jan	72.0	73.1	72.4	75.2
Feb	71.7	72.1	66.2	74.6
Mar	59.9	71.4	66.3	74.5
Apr	73.3	72.7	74.1	77.4
May	86.9	77.9	78.8	81.1

4.4 SHORT-TERM FLUCTUATIONS IN NATURAL LOW FLOWS AND EXTREME FLOW REDUCTION AS A POTENTIAL DISTURBANCE

4.4.1 Short-term patterns of natural and extreme low flows

The natural fluctuations in instantaneous discharge observed throughout the period spanning the dry season, as well as the changes in discharge at the three experimental sites (relative to the control site - the Elands) associated with manipulated reductions in flow, are illustrated in Figures 4.7a-d. Differences in discharge at the control locations of reaches of the Molenaars, Du Toits and Riviersonderend rivers, and for both locations at the Elands site, provided an indication of the natural variability in discharge within the same reach, during a single dry season. Discharges measured at impact locations indicated the reductions in flow achieved by experimental diversion. For the reasons discussed in Section 3.2.4, instantaneous discharges presented in Figure 4.7 were derived from measurements only at run cross-sections.

Natural flow patterns at the Elands site

Fluctuations in instantaneous discharge (Q_{inst}) from early summer (December) to the onset of autumn (May) were fairly low for the control site, from a low of 0.190 $m^3 s^{-1}$ (April) to a maximum of 0.361 $m^3 s^{-1}$ (December), indicating a fairly stable dry-season flow pattern (Figure 4.7a). The recorded discharge range represented a near doubling of baseflow within the study period (a factor of 1.9). Discharge was similarly low in the months of January to April, and only marginally lower than all other months in March (impact

location) and April (control location), with percentage reductions in magnitude relative to antecedent (early March) low flows of 5% and 6%, respectively. Increases in flow magnitude in May, with the transition to autumn, were in the order of 19% (as measured at the impact location) to 54% (control location). The latter discrepancy in range in Q_{inst} demonstrated the confounding influence of experimental error with discharge measurement (Section 3.2.4), as both locations should effectively be experiencing similar flows on the same day. A small volume of surface flow was observed entering the impact location from bank storage during most site visits. This may have contributed, in part, to the consistently slightly higher discharges recorded in this location relative to the control location (Figure 4.7a).

Comparison of Q_{inst} figures with average daily discharges from the historical flow record (Section 4.2) revealed differences in the months of minimum and maximum for the former relative to average daily conditions. Based on the results of an analysis of the monthly distribution of flows (see above), the month of the year of lowest flow is characteristically February, both in terms of flow volume and Q_{mean} (Figures 4.1 and 4.2b). Furthermore, highest flows over the six-month study period typically occur in May (Figure 4.2b). The degree to which the observed natural and unnatural flow patterns differed from established longer-term hydrological trends is explored further below.

Natural and experimentally manipulated flow patterns at the Molenaars site

Natural fluctuations in Q_{inst} natural from December-May were moderately low for the Molenaars site, ranging from 0.322 $m^3 s^{-1}$ in early March (and hence probably also February) to 0.721 $m^3 s^{-1}$ in December (a factor of 2.2) (Figure 4.7b). Measured flows were lowest in early March and only slightly higher in April, where the former observation was in accordance with the long-term flow pattern (Figure 4.2a). On the basis of historical data, however, May flows typically greatly exceed April flows, which in turn, usually exceed all baseflows from December to the end of March (Figure 4.2a and Appendix 4.1). The observed discharges therefore point to a naturally dry summer, possibly of protracted duration.

On average, on the basis of Q_{inst} figures, 36% of the total dry-season low flow was diverted from the river upstream of the impact location, during the experimental impact phase (Feb-Mar; Figure 4.7b). Hence, some 64% of natural flow remained in the river. The overall average proportional reduction in discharge, taking into consideration discharges measured during construction of the flow diversion weir, was estimated as 35% (Table 3.1). An increase in flow magnitude of *c*. 61% occurred in the impact location with the reinstatement of natural flows from March to April, during the post-impact phase. This was in contrast with a natural slight decrease in magnitude of 2% in the control location (Figure 4.7b). The pattern of low flows at the flow-impacted location remained otherwise unaltered from natural, with lowest flows being experienced in early March (0.210 $m^3 s^{-1}$) and therefore, probably in February, and the highest magnitude Q_{inst} occurring in December. A detailed comparison of short-term trends in natural and experimental flows with longer-term hydrological trends is made in Section 4.3.2.

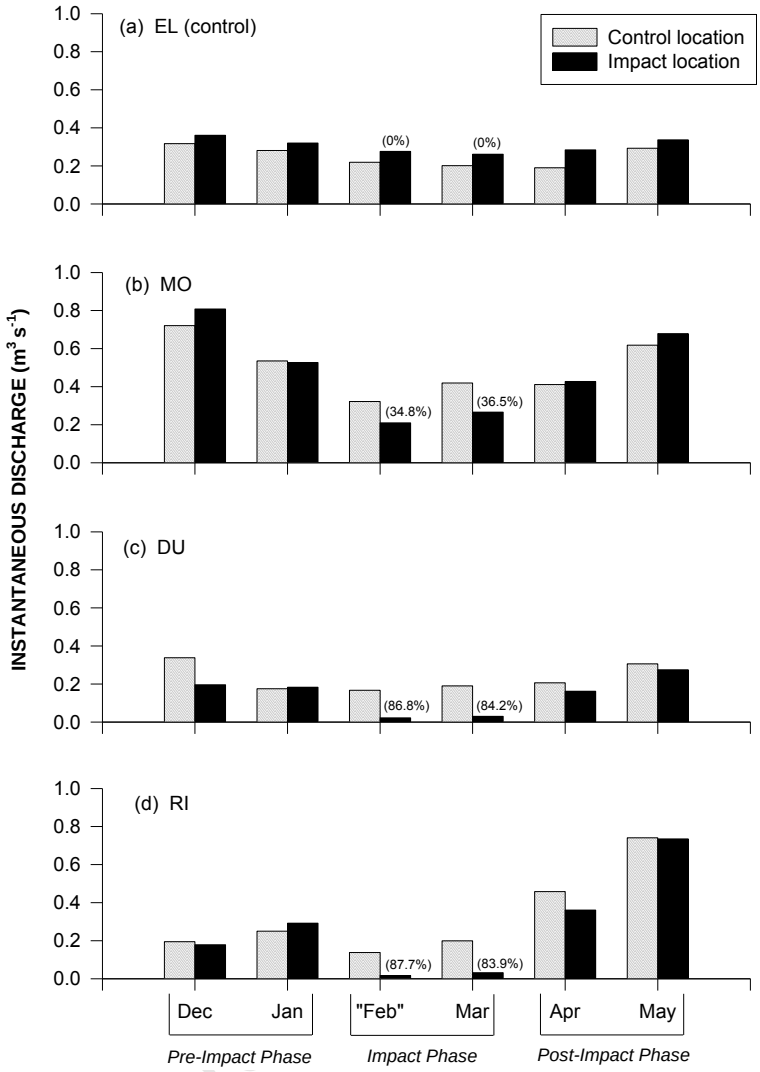


Figure 4.7 Instantaneous discharges ($m^3 s^{-1}$) for all study phases at the sites: (a) Elands; (b) Molenaars; (c) Du Toits; and (d) Riviersonderend. Percentage flow reductions are indicated in parentheses. Natural discharges are represented by control location figures, as well as those for the impact location before and after flow reduction. "Feb" discharge values for the Molenaars and Elands sites were recorded in early March, while all other sampling was completed in February.

Natural and experimentally manipulated flow patterns at the Du Toits site

Natural Q_{inst} figures were similarly low in the Du Toits River from January-April, indicating fairly constant dry-season low flows (Figure 4.7c). December and May discharges only marginally exceeded peak summer values. The lowest flow recorded was 0.167 $m^3 s^{-1}$, in February, and the highest Q_{inst} (0.338 $m^3 s^{-1}$) occurred in December (a relative increase of 2.0). An assessment of average total flow volumes and average daily discharges (Figures 4.1 and 4.2c, respectively) showed a similar pattern, with a gradual decrease and increase in flow at the ends of winter and summer, respectively. Moreover, the month of lowest flow, on the basis of the long-term hydrological record, corresponded with that in the short-term. However, from the historical

record, May average flows typically exceed those for December, due to an increased incidence of high flow events (Figure 4.2c and Table 4.3).

About 85.5% of the total dry-season flow was diverted upstream of the impact location, leaving only 14% of natural flow (Figure 4.7c). The overall average proportional reduction in discharge, taking into consideration discharges measured during weir construction, was estimated as a lower 80% (Table 3.1). A relative increase of *c*. 440% was experienced in the impacted reach with the reinstatement of natural flows in April, in comparison with the natural increase in Q_{inst} of only 8% (Figure 4.7c). Apart from a reduced magnitude and extended duration during the impact phase, the pattern of low flows remained unaltered from natural (i.e. lowest flows experienced in February; 0.022 $m^3 s^{-1}$). Further comparison of short-term flow trends in relation to the historical flow regime takes place below.

Natural and experimentally manipulated flow patterns at the Riviersonderend site

Natural flows (Q_{inst}) at the Riviersonderend site were variable, ranging from a minimum of 0.138 $m^3 s^{-1}$ in February to 0.741 $m^3 s^{-1}$ in May (Figure 4.7d). This range represented an increase factor, from minimum to maximum, of 5.4. January Q_{inst} was higher than that of adjacent months, possibly as a result of a dry-season fresh event, while February was the month of lowest flow. Comparison with the historical flow record (Figure 4.2d) showed that February is typically the lowest flow month of the dry season. However, the longer-term pattern differed somewhat from that in the short-term, with a progressive, consistent decrease in low flows from early spring through summer. Slight, gradual increases in flow characteristically occur from March to April, and there is a marked increase in total flow volume and average daily discharge in May (Figures 4.1 and 4.2d). The latter pattern was reflected in the flow data collected in this study.

Marginally more flow was diverted from the Riviersonderend reach than the Du Toits reach, at *c*. 85.8% of the total dry-season flow (Figure 4.7d). Only 14% of the natural flow thus passed through the impact location. The overall average proportional reduction in discharge, taking into consideration discharges measured during construction of the flow diversion structure, was estimated as a higher percentage (82%) than that of the Du Toits reach (Table 3.1). The river was subjected to an increase in Q_{inst} of about 1028% with the reinstatement of natural flows in the impact location, in April. This contrasted markedly with a natural flow increase of 130% (Figure 4.7d). As for the other sites, the characteristic dry season pattern in the impact location remained unchanged from natural, with the lowest flows being experienced in February (0.017 $m^3 s^{-1}$). Natural and unnatural short-term fluctuations in discharge are compared with a series of hydrological indices based on the historical flow record in Section 4.3.2.

Summary comparisons among sites

For all sites, lowest, natural instantaneous flows tended to occur from February until early March. In all instances, except the Riviersonderend, highest Q_{inst} figures were recorded in December. At the Riviersonderend site, elevated May flows reflected the earlier transition to winter conditions at this site

(Section 2.4). The Riviersonderend River also showed the most variable flow pattern, with an increase in low flows from December-January, and a subsequent decrease to naturally very low flows in February. Three of the sites showed a magnitude range of baseflows throughout the experimental period in the order of a factor of two, while the Riviersonderend site exhibited a far greater degree of change in flow. The natural May flow in the Riviersonderend River was greater than the highest Q_{inst} recorded for the Molenaars, even though the latter is a far larger river at the site. However, as the discharges are instantaneous, higher flow events at the Molenaars and other sites could have occurred on other sampling dates. Discharge magnitudes for days other than sampling dates are only known for the two sites for which hydrological gauging was ongoing (Table 2.2), so a comparative, rigorous analysis of the possible influence of antecedent flows was not feasible. It was evident from gauged data for the Molenaars site, however, that the unnaturally low flows remained roughly constant throughout the two months of the impact phase. At the Du Toits and Riviersonderend sites, artificially reduced low flows were also likely to have been near-constant at the figures recorded for February and March, due to the structure of the temporary diversion weirs (Section 3.1.2). In terms of experimental flow reduction, the greatest magnitude discharge was diverted at the Riviersonderend, closely followed by the Du Toits and then the Molenaars sites, with very similar extended low flow durations of nearly two months in all cases (Section 3.1.3; Table 3.1).

4.4.2 Linking short-term trends in flow regimes with low flow indices: extreme flow reductions as disturbances

Short-term flow fluctuations experienced at each site were placed in the context of the natural, historical hydrological disturbance regime (described in Section 4.3) using select flow indices (viz. Q Mean Mean; Q Median Median; Median Q7d-low; Q Min Min), as well as flow percentiles calculated from monthly FDCs, in particular Q_{95} (Section 4.3 and Appendix 4.1). The Q_{95} was selected preferentially over other percentiles in the range Q_{75}-Q_{99} (the typical range of flow percentiles for low flow assessments; Smakhtin 2001), as it showed the most consistent trends, both within those months corresponding with the study period and among sites (Section 4.3.3; Figure 4.5). Explanations of the various flow indices are provided in Section 3.2.3 and Table 3.2. The maximum daily average discharge for each month over the historical record (Q Max Max - Table 4.3) far exceeded the magnitudes of the other indices for all sites and, therefore, was not considered further.

Instantaneous discharges expressed as flow percentiles

As a first step in directly relating observed discharge patterns over the study period to the historical hydrological regime, instantaneous discharges measured in the field were expressed as flow percentiles, using the corresponding monthly FDC for each site (Figure 4.8a-d). Percentiles equal to or lower than Q_{50} represented the approximate boundary between low- and high-flow regimes.

In assessing percentile ranges represented by the instantaneous discharges, it was necessary to be cognisant of two factors. Firstly, Q_{inst} values within the two locations at a site in the same month naturally differed as

they were not recorded on the same day in all cases (e.g. the Elands Q_{inst} values for the two locations in April were recorded two weeks apart). So, corresponding flow percentiles were expected to differ somewhat, reflecting natural within-month fluctuations in daily discharge. In the most extreme case recorded, natural December discharges for the two Du Toits locations were calculated as representing the Q_{29} and Q_{86} (Figure 4.8c). In this case, an average figure, the 58th percentile, was used for discussion purposes. In all other cases, where the flows at both locations should have been highly similar, but practically were not measured as such (Figure 4.7), both values are presented (control/impact percentile). Secondly, there is a known tendency for high experimental error in measurement at low flows (Section 3.2.4). For example, under control conditions (Figure 4.8a), the two Elands locations clearly differed in recorded discharge, with percentiles at the control location far lower than those reflecting flows in the impact location.

The flow regime at the Elands site represented a narrow overall range of percentiles from the 86/68th in January to 96/75th in April (Figure 4.8a); it is more likely that the higher (control) percentiles more precisely reflect field conditions. Generally, river flows were within the lower spectrum of possible flows (as per the site's flow history) in any one month, especially in December and May. At the Molenaars site (Figure 4.8b) discharges in December and January fell just below Q_{75} levels, with a shift to flows of higher exceedence as summer progressed. During the impact phase of the study, the river was naturally experiencing low flows in the order of the 96th (February) to 87th (March) percentiles (Figure 4.8b). The experimental flow diversions of 34.8% and 36.5%, respectively (Figure 4.7b) effectively reduced flows in these months to the 99th-100th percentiles – i.e. below the lowest flow that the river had been exposed to naturally in the long term. Examination of the relationship between Q_{inst} values and corresponding percentiles for the Du Toits site (Figure 4.8c) suggested that flows during the study period fell within Q_{30} to Q_{75}. Natural flows during the impact phase of the study were relatively high for the middle of the dry season (Q_{56} and Q_{32} for February and March, respectively; Figure 4.8c). In contrast, the approximately 85.5% reduction in flow in impact location (Figure 4.8c) resulted in flows of 100% exceedence in both months (Figure 4.8c). Thus, flow reduction to levels below those ever having occurred historically was achieved. For the Riviersonderend site (Figure 4.8d) flows occurring naturally in the river over the study tended to be relatively high on the basis of the historical flow record, especially in January (32/26th percentile flows). During the February and March, Q_{inst} figures for the control location were equivalent to Q_{68} and Q_{50}, respectively (Figure 4.8d). The *c.* 85.8% flow reduction in the impact location represented an exceedence value of 100% in both these months. Hence, the magnitude of the low flow disturbance was extreme, below that ever recorded historically.

Links between instantaneous discharges and low flow indices

The above results provided a first indication of the relationships between natural flows over the duration of the study and the historical regime, in addition to demonstrating that all experimental reductions in flow represented potentially severe disturbances to the rivers. Further evidence was provided by examining the degree of correspondence between the flows measured on site and standard low flow indices (Figure 4.9; see Section 3.2.3 and Table 3.3, for derivations of flow indices). Average discharges for each month, over the

period of record (Q Mean Mean), provided an upper bound to the envelope of flow indices, for the purpose of comparison.

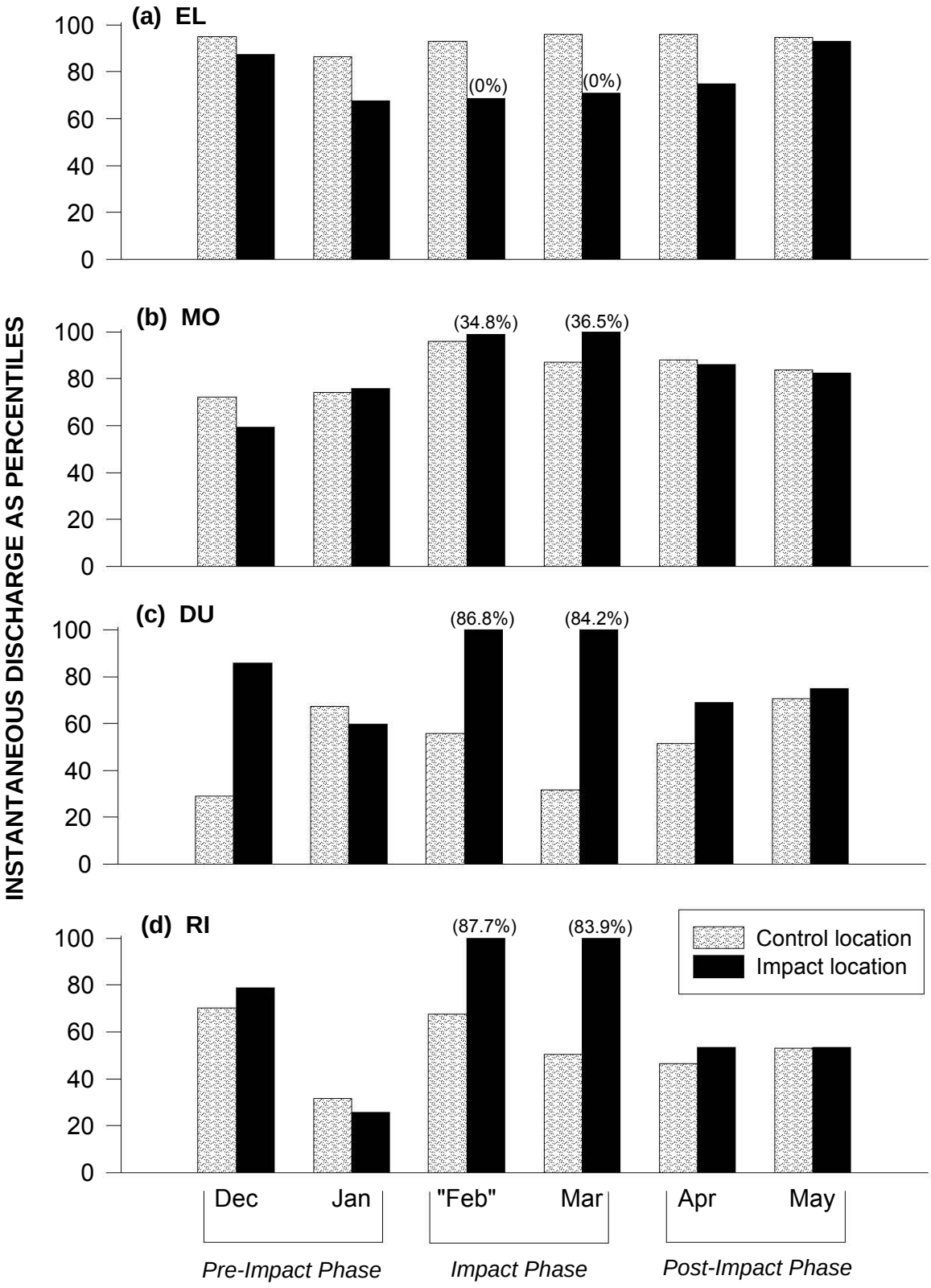


Figure 4.8 Instantaneous discharges expressed as flow percentiles derived from corresponding monthly FDCs, for the duration of the study, at the sites: (a) Elands (control site); (b) Molenaars; (c) Du Toits; and (d) Riviersonderend.

For the Elands site, natural Q_{inst} figures formed a narrow envelope from just above the monthly median Q7d-low values to just below the Q_{95} values, approaching the absolute minimum historically recorded in April (Figure 4.9a). Although small fresh events probably occurred outside the times of sampling, in response to localised storms (pers. obs.), these results suggest that the summer was drier than average and protracted, with naturally low flows throughout the study.

Figure 4.9b allows comparison between the pattern of flows experienced during the study and low flow indices, for the Molenaars site. Under conditions of natural flow (control location), measured discharges typically were found to lie between Q7d-low and Q_{95} figures, except during December when flows tended towards the historical Q Median Median. Additionally, in the peak dry season, observed flows were marginally lower than the corresponding Q_{95} index. These results supported earlier evidence that natural peak dry season flows were lower than average. The extreme discharge reduction from February to March (impact location) drove flow magnitudes to below absolute minima on record (as also shown above). Hence, the river and its biota were subjected to a flow disturbance that qualified as extreme in magnitude, and duration, relative to the long-term, natural disturbance history of the site.

Comparison of the observed pattern of flows for the Du Toits River, with the suite of hydrological indices showed that Q_{inst} figures fluctuated from just above the median (Q Median Median) to just below the Q7d-low flow (Figure 4.9c). In the lowest flow month of February, when these two indices were most similar, the measured natural discharges fell between them, suggesting that river flow tended to be low at that time, but not markedly so. The experimental reduction of flow during the study impact phase generated extreme low flows, significantly lower than even the absolute minima on record for February and March (Figure 4.9c). As a result, the experimental reduction in dry-season flow represented an extreme event not experienced previously in the river, in magnitude or duration.

During the study, natural discharges in the Riviersonderend reach did not bear a consistent relationship with any particular hydrological index over December to May (Figure 4.9d). Flows varied from just above Q7d-low in December to well above the long-term median (Q Median Median) in January. Thereafter, there was a decrease in discharge to between the Q7d-low (Feb) and median in March. The shift to autumn conditions from April onwards was most pronounced at this site, with Q_{inst} figures closely matching the median index. Thus, as in the case of the Du Toits, the general trend of a drier than usual summer observed for the Elands and Molenaars sites, was less apparent at this site. The experimental diversion of flow from February to March (impact location) reduced river flow to below the corresponding absolute minima on record (Figure 4.9d). Therefore, the unnatural flows represented a potentially extreme low-flow disturbance event for the system.

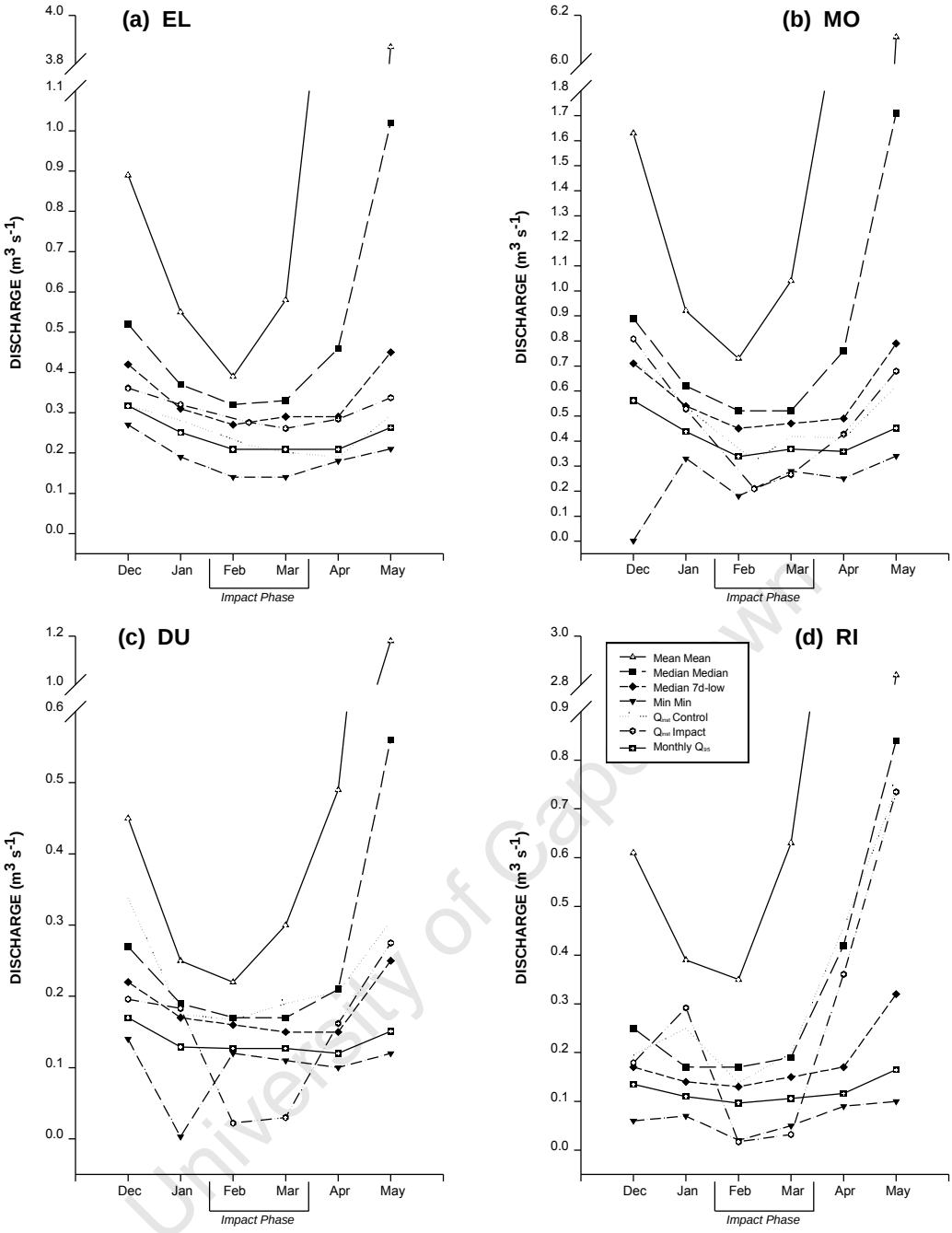


Figure 4.9 Comparison of natural instantaneous discharges (Q_{inst}; m^3 s^{-1}) with various flow indices, for site control and impact locations during the study period. (a) EL = Elands; (b) MO = Molenaars; (c) DU = Du Toits; and (d) RI = Riviersonderend. For the February trip, Q_{inst} values were recorded in early March for the EL and MO sites. Scale breaks are indicated for Q Mean Mean.

4.4.3 Characterizing flow variables in terms of potential ecological relevance

The results of a PCA of 32 different flow variables (a reduced data set to minimise redundancy; Section 3.2.3), reflecting the low flow regime and, to a lesser extent, general and high flow regime features of the four sites, are presented in Table 4.9 and Figures 4.10a, b. The multivariate ordination was used to characterize flow variables with particular group affinities in terms of their potential ecological relevance.

Coupled with the findings of previous sections, they also assisted in clarifying the main differences among sites in hydrological disturbance history and in identifying an appropriate subset of flow indices for examining invertebrate response to low-flow disturbance in later chapters.

Table 4.9 Loadings of flow variables for principal components PC1-PC3. See also Figure 4.10. Where appropriate, variables were standardised by Q_{50} for inter-site comparisons [std]. 'Dry' represents the peak low flow months of Jan-Mar.

	PC1	PC2	PC3
Eigenvalue	16.4	10.3	5.3
Explained variance (%)	51.3	32.1	16.6
Flow variable (abbrev.)			
Annual flow volume (Vol) [std]	0.80	-0.60	0.01
Dry season flow volume (VolDry) [std]	0.81	0.38	-0.46
Average of instantaneous discharges (QinstM) [std]	0.72	0.65	-0.24
Predictability (P)	-0.69	-0.73	0.00
Constancy (C)	-0.53	-0.85	-0.04
Contingency (M)	0.21	0.97	0.11
Dry season P (PLow)	-0.95	0.06	0.30
Dry season C (CLow)	-0.94	0.29	0.20
Dry season M (MLow)	-0.29	-0.83	0.47
Annual coefficient of variation (CV)	-0.03	-0.97	-0.25
Dry season CV (CVDry)	0.87	0.14	-0.47
CV for February (CVFeb)	0.95	0.30	-0.02
CV of annual minimum discharges (CVQMin)	-0.31	-0.81	-0.49
CV of annual median 7-day low flows (CV7dLow)	-0.10	-0.87	-0.48
Index of inter-annual variability of peak floods (IV)	0.99	-0.04	0.13
Flood of 1:2 year average return interval (ARI1:2) [std]	0.60	-0.70	0.39
Discharge exceeded 5% of the time (Q5) [std]	0.97	-0.26	0.03
Mean daily discharge (MDF) [std]	0.86	-0.35	-0.37
Minimum discharge (QMin) [std]	-0.25	0.15	-0.96
Mean annual minimum discharge (MAM) [std]	-0.96	-0.23	-0.16
Maximum annual discharge (QMax) [std]	-0.19	-0.91	-0.36
Median 7-day low flow (7dLow) [std]	-0.70	-0.53	-0.48
Median discharge (Q50)	-0.19	-0.45	0.87
Median dry season discharge (Q50Dry)	-0.29	-0.49	0.82
Discharge exceeded 80% of the time (Q80) [std]	-0.81	-0.25	-0.53
Dry season discharge exceeded 80% of the time (Q80Dry) [std]	-0.83	0.44	0.36
Discharge exceeded 90% of the time (Q90) [std]	-0.90	0.28	-0.35
Dry season discharge exceeded 90% of the time (Q90Dry) [std]	-0.84	0.49	0.24
Discharge exceeded 95% of the time (Q95) [std]	-0.97	0.16	-0.17
Dry season discharge exceeded 95% of the time (Q95Dry) [std]	-0.84	0.53	0.10
Discharge exceeded 99% of the time (Q99) [std]	-0.87	0.26	-0.41
Dry season discharge exceeded 99% of the time (Q99Dry) [std]	-0.52	0.80	-0.29

The first two principal components of the PCA explained a high 83% of the total variance in the flow variables (Table 4.9). Based on the loadings of individual variables (particularly where correlation coefficients between variables and PC1 and PC2 were high, > 0.8) it was possible to delimit three main

groups of flow variables, two with several subgroups, loosely corresponding with general (Group 1), low flow (Group 2), and high flow (Group 3) characteristics of the flow regime (Figure 4.10a).

The main separation of flow variables along PC1 was driven by flood magnitude and variability, with particularly high positive loadings for IV and annual Q_5 (Group 3), as well as peak dry-season flow variability and magnitude (Group 2b) at one end. This was coupled with the magnitude of moderately low flows (Group 2c), plus magnitude and predictability of very low flows (Group 2a), at the other extreme of the axis. Of the low flow variables, the main negative loadings on PC1 could be attributed to Q_{95} and MAM, as well as several other highly inter-correlated indices (including annual and dry season flow percentiles, Q_{80} to Q_{99}). The separation of Q_{99Dry} and ARI1:2 diagonally across the plot further highlighted the low and high flow endpoints of the overall flow regime. Further separation of flow indices, along PC2, was mostly as a function of the clear divergence between a group of measures of overall flow variability (Group 1a), especially annual CV and Q_{max}, and low flow variability (e.g. CV_{QMin}, CV_{Q7dLow}) with high negative loadings, and flow contingency (*M*; Group 1b), with the highest positive loading on PC2 of all indices.

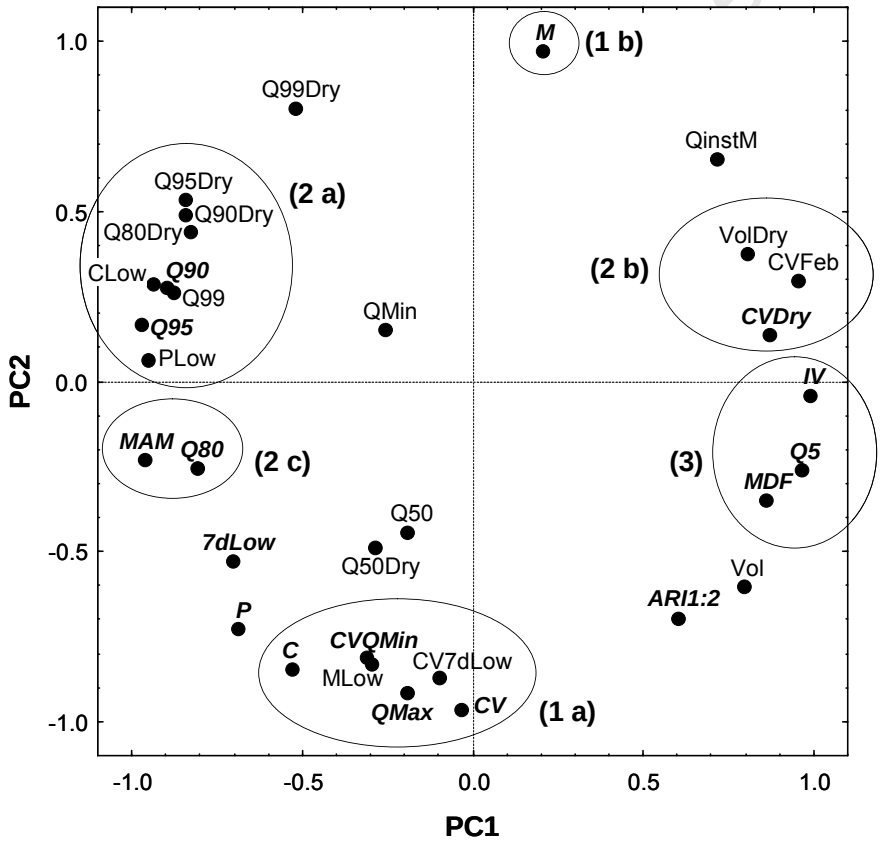


Figure 4.10 (a) Loadings of the flow variables for the first two principal components (PC1 and PC2). Dashed ellipses delimit the main flow variable groups/subgroups. Variables in bold italics represented the most useful subset of flow indices for site separation. Abbreviations as per Table 4.9.

Of the full suite of flow variables, several indices from the general, low flow and high flow regime categories were particularly influential in separating the four sites on the basis of their hydrological character (as indicated in bold italics in Figure 4.10a), namely: MDF, *P*, *C*, *M*, CV, CV_{QMin}, CV_{Dry}, MAM, Q_{80}, Q_{90}, Q_{95}, 7dLow, Q_{Max}, IV, Q_5, ARI1:2.

A plot of the site loadings on PC1 and PC2 revealed the distinctly different hydrological character of the Riviersonderend River as compared with the other three sites (Figure 4.10b). It also pointed to somewhat greater similarity between the Elands and Molenaars flow regimes, than between each regime and that of the Du Toits site. The Riviersonderend River was strongly characterized by the relatively high variability and low predictability of its low flows, mid-dry season, as well as the relative flashiness of its high flow regime. The Du Toits was more weakly influenced by wet years and peak flow events than the Riviersonderend, in particular, and exhibited the most stable, distinct low flow regime (and hence, low-flow disturbance history) of all study sites. The flow character of the Elands reach appeared most strongly affected by fairly predictable, but high annual flow variability (high correlations with CV, CV_{Qmin} and P), supporting earlier findings. On the basis of site loadings, the Molenaars River exhibited the most moderate hydrological disturbance history of all sites.

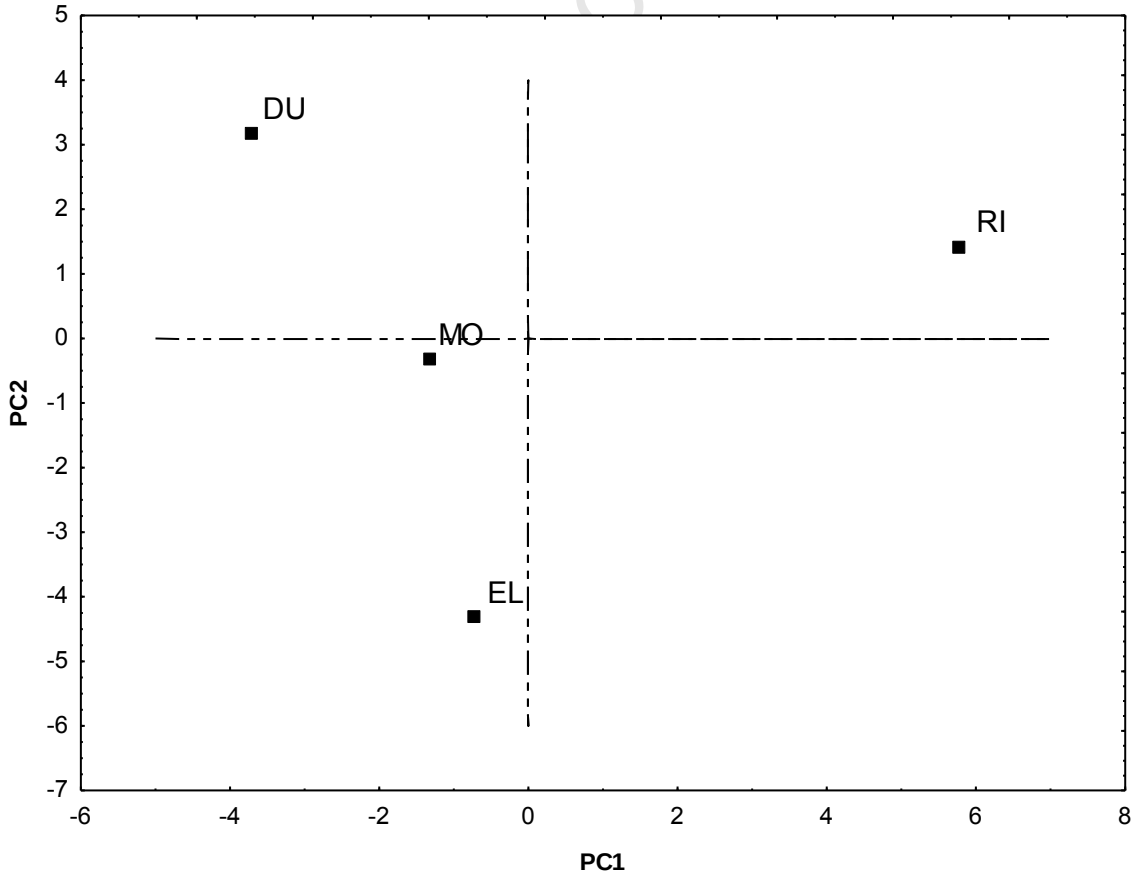


Figure 4.10 (b) Site loadings for PC1 and PC2.

4.5 SUMMARY AND DISCUSSION

4.5.1 Comparison of the natural flow disturbance histories of the sites

Overall hydrological character

Broad-scale analysis of the flow regimes of the four rivers at the study sites confirmed, as based on the hydrological classification by Joubert and Hurly (1994) and pilot analysis, that all rivers are within the 'winter peak flow' region of the country (Section 2.1.2). Further, despite clear differences in size, and corresponding MARs and flow volumes among the sites, from the comparatively large Molenaars River to the smallest, the Du Toits River, all flow regimes are perennial and of a 'winter moderate' type (Joubert and Hurly *op. cit.*). Although draining the smallest catchment, the Riviersonderend River exhibited the highest runoff coefficient overall and comparatively high event responsiveness (*sensu* Richards 1990), reflecting its mountain stream character. Comparison of flow distribution patterns at several temporal scales also demonstrated that all study reaches are subjected to a similarly distinct, seasonal flow pattern characterized by summer low flows, coupled with a flood-dominated winter. The Elands site was found to reach peak flow volume slightly earlier in the winter than the other sites, and with relatively high flood flashiness at that time of year. The Riviersonderend reach, in contrast, showed distinct variability in higher flows during drier months.

Characteristic low flow regimes

Characterization of low-flow disturbance required detailed investigation of areas of similarity or difference in low flow regimes, within the general low flow period shared by all study reaches. The dry season typically extends from about November to early April, with January to March representing the window of lowest flow (i.e. 'peak dry season') for all sites except the Riviersonderend (where December average discharges were marginally lower than those of March). The increased influence of fresh (elevated flow) events with the shift from summer to autumn appeared most and least gradual of all sites for the Du Toits and Riviersonderend rivers, respectively.

Scrutiny of historical flow regimes revealed that even in a region with a hydrologically well defined dry season, some measure of individuality in terms of low flow character was apparent each month, and for each site. Importantly from a flow disturbance perspective, though, February was the most consistently stable month in terms of natural lowest flows, with the narrowest discharge amplitude occurring in this month for all sites; similarly low ranges in discharge were observed for the adjoining months of January and March. Lowest mean low flows occurred in the Du Toits reach ($Q_{mean} < 0.6$ m^3 s^{-1}), while the Molenaars reach experienced the highest discharges of all sites during February, though still with average discharges below 2.0 m^3 s^{-1}.

All sites exhibited some variability in the times series of natural, extreme low flow events, reflecting a key aspect of their flow disturbance history, particularly outside the peak dry season and in the cases of the Elands and Molenaars rivers. February minima typically were the lowest of all months and stable across the period of record. Values above the long-term February median, and extremely low minima, were infrequent. Flows reached very low levels more frequently in the Du Toits and Riviersonderend reaches than at the other sites. The observed compression of the low flow regime of the Du Toits River conferred long-term stability, though the reach had been subjected to the lowest natural minimum discharge on record of all sites. The Riviersonderend River's pattern of flow minima was less regular that for the other sites, with a wider range. This lower temporal stability of very low discharges was supported by the river's naturally high flow variability and low flow predictability, discussed further below. Extreme, low flow events remained relatively sporadic in the Riviersonderend reach, however, as for the other reaches, with only one instance historically where flows dropped exceptionally low. Given the known lack of accuracy in measurement at very low flows (Gan and McMahon 1990b; Gordon *et al.* 1992), as for floods (Section 3.2), however, such flow outliers from gauging station records were treated with caution.

Patterns in annual low flow percentiles were similar across the sites (except for Q_{99}, as a measure of extreme events) with a narrow band of discharges representing the flows equalled or exceeded 75 to 95% of the time within the main low flow season. Differences in actual flow magnitudes represented by February flow percentiles were particularly small, with the narrowest amplitude apparent for the Du Toits site, mirroring its comparatively stable low flow history. The converse pattern was apparent for the Riviersonderend River, again corresponding well with the site's more variable low flow regime. Irrespective of the river concerned, little difference was observed between the flow magnitudes represented by Q_{75} and Q_{80}, or the flow percentile pair of Q_{90} and Q_{95}, with greatest convergence during the lowest flow months occurring for the former pair of indices. The Q_{95} (in contrast to the more variable low flow index, Q7d-low) appeared to be a potentially useful descriptor of flow disturbance, because it showed the most consistent trends of all low flow indices within those months corresponding with the study period and among sites. While demonstrating utility in this role, the index (and Q_{90}) are within the realm of flow percentiles representing drought flows (Petts *et al*. 1999; Nathan and McMahon 1990a; Gordon *et al.* 1992), rendering their suitability as flows for ecological maintenance questionable, as argued by several authors (e.g. Cassie and El-Jabi 1995; Tharme 1996; Petts *et al.* 1996). Regardless, it appears that Q_{95} has become well established as a low flow measure for ecological impact assessment and environmental flow purposes (Section 4.1), including habitat maintenance for riverine biota (e.g. Gustard 1979; Gustard and Bullock 1991; Armitage and Petts 1992; Petts *et al.* 1995; Gippel and Stewardson 1998; Dacova *et al*. 2000; Agnew *et al.* 2000). In the U.K., for instance, Q_{95} is the most commonly used low flow index for recommending ecologically acceptable flow regimes, although Q_{90} has also been used (Tharme 2003; Acreman and Dunbar 2004; Bragg *et al.* 2005). The virgin Q_{95} for the four driest months of the year was used by Gippel and Stewardson (1998) as a low flow index, in an Australian assessment of the Wetted Perimeter method for defining environmental flows.

Despite the above consistency in percentile trends, comparative analysis of flow duration curves at different temporal scales revealed the merit of using the particular low flow index that best corresponds with the temporal scale of assessment (a point also made by Petts *et al.* 1996). Individual flow percentiles specific to each of the low flow months studied were more meaningful measures of flow disturbance than annual ones. This distinction became especially important during the peak dry months, when differences between annual and monthly low flow indices were most pronounced and where slight differences in discharge markedly influenced percentile values.

The differences in low flow regime detected across the sites, though often subtle, highlighted the importance of understanding and independently characterizing the low flow patterns of individual rivers, before attempting to meaningfully compare flow disturbance regimes or assess their potential ecological implications. This is even relevant, as in the current study, where rivers are within the same biogeographic region or catchment, and of the same general flow type. Smakhtin *et al.* (1995) in analyses for some 240 flow gauging stations recording near-natural flows on South African rivers found that low flow regimes were highly dependent on local physiography and exhibited considerable spatial variability. Many of the low flows indices studied exhibited a similar pattern in space, however, suggesting, as corroborated through further analysis (Smakhtin and Toulouse 1998), that they were strongly interrelated. Agnew *et al.* (2000) found that despite catchments that were naturally alike, the English Bulbourne and Gade rivers exhibited quite different low flow regimes, both in terms of a range of low flow indices, such as Q_{min}, Q_{95} and MAM7, and their degree of sensitivity to low flows. Monk *et al.* (2006) reached a similar conclusion in a study linking flow variability and invertebrate community response across U.K. rivers (see also Chapter 8), where the results obtained, especially for low flow regimes, reinforced the importance of understanding flow variability even within small geographic regions.

Flow regime variability and predictability

Hydrological variability and predictability were clearly relative characteristics, as also observed by Clausen and Biggs (1997), with various measures of overall and low flow variability, as well as flow predictability, resulting in different orders of ranking for the four rivers. This was irrespective of the fact that the reaches were in fairly close proximity geographically, experienced flow regimes of the same fundamental type, and were all small to moderately-sized upper river sections. The results highlighted both the importance and complexity of using multiple indices of flow variability in an analysis of hydrological regimes, as well as the need for clarity on the reason for selection of any particular index or indices.

Of the various measures of flow variability compared across sites, the overall coefficient of variation of mean daily flows, annual CV, commonly has been identified as one of the most ecologically relevant flow indices, as well as a particularly appropriate index for differentiating among flow regimes (Hughes and James 1989; Biggs *et al.* 1990; Jowett and Duncan 1990; Richards 1990; Clausen and Biggs 1997, 2000; Hughes 2001; McMahon and Finlayson 2003; Smakhtin *et al*. 2004; see below). Typically, it has been

assumed that a high annual CV is indicative of a naturally disturbance prone river, in which therefore, the biota might be expected to be more tolerant of more extreme flow alteration. Coon (1987, cited in Poff and Allan 1995), for example, found an apparent correlation between flow variability and seasonal disturbance intensity in streams of the midwestern U.S.A. In characterizing the variability of 78 streams using 11 flow indices (Section 4.1), however, Poff and Ward (1989) found that single non-temporal (annual CV) and temporal (*P*) measures of overall flow variability explained very little of the variability in flood disturbance characteristics, on the basis of pairwise correlations among flow indices. Furthermore, Biggs *et al.* (1990) cautioned that as high and low CVs may be associated with vastly different underlying streamflow patterns, CV might not be particularly useful in understanding ecosystem response to flow disturbance where the range of flow regimes under study is wide (not the current case). It is therefore clearly important to be explicit as to which aspects of the flow regime are principally responsible for the observed flow variability when attempting to link CV and biotic response.

Overall hydrological variability (annual CV) was high for all the sites in this study, given the relative predictability and low variability of the southwestern Cape as a hydrologic region (King *et al*. 1992; Section 2.1.2), though still of the order expected for dryland South African rivers (Gordon *et al.* 1992; Davies *et al.* 1993; Puckridge *et al*. 1998; Thoms and Sheldon 2000). Such levels of hydrological variability, and associated extreme flood and drying disturbances, have led local researchers to suggest that the country's rivers might be inhabited by less structured biotic assemblages, dominated by hardy opportunists, than the more predictable, less variable rivers of the Northern Hemisphere (O'Keeffe *et al.* 1989b; Davies *et al.* 1995). Despite being of the same flow regime type, differences in general patterns of flow variability based on annual CV were obvious among the sites, with the Elands and Du Toits rivers possessing the highest and lowest annual flow variability, respectively. Poff (1996) reported a more marked similarity in CV (and *P*) values for streams considered of the same hydrological type, with significant differences in CV and *P* more typical across diverse stream types. Interestingly, in the present study, monthly CVs based on flow volumes showed a tendency at the sites (except for the Riviersonderend) for lowest monthly flow variability to occur in the winter, generally followed by the month of lowest flow, February. Maximum monthly variability, in contrast, occurred in March for all sites except the Elands, where variability peaked slightly later. The implications of these patterns for the degree of low-flow disturbance to which invertebrates have been subjected over time would require further research. The patterns did highlight a possible shift in disturbance intensity from mid- to late-dry season. Further, they raised questions about some of the assumptions made about the relatively higher degree of disturbance occurring in high flow than low flow periods of the year.

Specifically in terms of the comparative potential for low-flow disturbance and hence, invertebrate response to extreme flows, highest flow variability in the lowest flow month (February CV) and for the peak dry season (i.e. three lowest-flow months; 'dry period' CV) were recorded for the Riviersonderend reach (despite historically stable one-day minima). In contrast, February and peak dry season flow variability were lowest for the Du Toits and Molenaars reaches, respectively. It proved more difficult to discern clear patterns for

the other indices of low flow variability examined (CVs for Qmin and Q7d-low), though the Elands site tended to show the highest levels of variability across them.

In addition to general measures of flow variability, Resh *et al*. (1988) suggested that comparative studies of physical disturbance effects in rivers consider their temporal pattern, and that indices such as Colwell's predictability (*P*) provided a useful approach in this regard. Several river ecohydrological studies have used such indices of flow predictability (almost exclusively *P* and its constituents, flow constancy, *C*, and contingency, *M*), alongside indices of flow variability, in this way, among them, Bunn *et al.* (1986), Resh *et al*. (1988), Poff and Ward (1989), Rader and Ward (1989), Poff and Allan (1995), Poff (1996), Thoms and Sheldon (2000) and Clausen and Biggs (1997, 2000). For example, in a comparison of natural and present-day flow regimes for the Barwon-Darling River, Australia, an increase in the predictability of flows (increases in *P* of 15-34%), mostly due to increased consistency, occurred with major hydrological alteration due to water resource development (Thoms and Sheldon 2000).

Despite quite distinct differences in overall flow variability, flow regime predictability was similar across the sites on the basis of Colwell's *P* (0.4-0.5). Flow constancy (*C*) patterns tended to match those of predictability more closely than did flow contingency (*M*). Highest regime predictability was apparent for the Elands site (a feature also supported by multivariate ordination), a result which, when coupled with the strong positive correlation between annual CV and *P*, suggested that the variability of the site's flow regime encompassed predictable elements. Predictability was lowest for the Riviersonderend site, principally due to low levels of among-month flow constancy that complemented the river's high flow variability. Flow predictability calculations that emphasised the low flow component of the flow regime, a less arbitrary delineation of flow states (and as such, recommended by Poff 1996), were less consistent than for the overall analysis. They still extended over a narrow range of values across sites, however, and with the Riviersonderend River remaining the least flow predictable river.

Clausen and Biggs (2000) also illustrated that despite annual hydrographs of quite different character and with a wide range in annual CV, three New Zealand perennial rivers exhibited narrow ranges of flow predictability and constancy. Resh *et al*. (1988), in addition to comparisons of flow variability based on the distributions of monthly discharge maxima and minima, used Colwell's indices to compare the degree of hydrological predictability, and by implication, degree of flow-related disturbance, of three streams in the United States. The outcome clearly illustrated the complexity in monthly patterns of predictability, as well as in the relative contributions of flow constancy and contingency to *P*. Important in the context of flow disturbance in the current study, Resh *et al*. (1988) further demonstrated that the high and low flow components of a river's flow regime could exhibit quite different levels of predictability, with monthly minima typically more predictable than maxima. Of the three rivers they studied, Blue Beaver Creek showed the most variable flow regime in terms of predictability (P) and constancy (C) of monthly maxima, which were lowest of the three sites (0.31 and 0.12, respectively), while contingency was intermediate.

However, the creek showed a markedly higher predictability of minimum flows than maxima, due to flow constancy. Halfmoon Creek had a more regular flow pattern that Blue Beaver Creek, with intermediate levels of predictability and constancy, but maximum contingency of monthly maxima across the three sites. Monthly minima for Halfmoon Creek were of higher constancy and lower contingency than the monthly maxima, though predictability was similar. Dismal River exhibited a constant flow pattern with low seasonality and temporal variability in monthly maxima. Predictability (0.99) and constancy (0.98) of monthly maxima were correspondingly highest of all sites, and contingency (M) lowest at only 0.01; values for monthly minima were similar.

Poff (1996), in an assessment of the degree of sensitivity of flow predictability (*P*) and variability (CV) (as well as flood timing) to the daily to annual hydrological time steps used in their calculation, using a subset of 118 streams across ten types for the continental U.S., found that temporal resolution affected *P* more than CV. Predictability was invariant, or gradually and consistently increased across the time steps examined, or was greatest at monthly scale. Hence, relative differences among streams in flow regime predictability might change depending on the time scale adopted. The CV of streamflow, in contrast, was consistently maximal at daily scale, with some streams showing minimum variability at monthly or seasonal scales. Moreover, a fairly high inverse correlation was found between CV and P at the daily time step, leading to the suggestion by Poff (1996) that CV might suffice as a single, and less arbitrary, descriptor of stream flow variability. In the current study, in contrast, the CV-*P* relationship across four sites of the same hydrological type was fairly strongly positive.

Further investigation certainly is needed into the absolute ecological relevance of the comparatively small relative differences in *P* (and its component indices) shown in this and other studies (e.g. Clausen and Biggs 2000). As the way in which flow states are defined has been shown by Poff (1996) to affect the relative differences in *P* across streams, there remains a need to standardize the method of index calculation in this regard. Ranges of values of flow predictability from other studies, against which to compare present results in terms of the sensitivity and potential ecological meaning of the index are few, and perhaps of limited use given they were derived for rivers of different biogeographical and hydrological types (e.g. Resh *et al*. 1988). Moreover, although some authors have questioned the suitability of Colwell's predictability index for hydrological analyses (Gan *et al*. 1991; Walker *et al*. 1995; Poff 1996; Puckridge *et al*. 1998), to date there remain few attempts to validate the results obtained using such indices in flow characterization studies. Results for this study were, therefore, treated with circumspection.

4.5.2 Identifying extreme low flows as potential pulse disturbances

It was essential that the natural, instantaneous low flows and specific experimental flow reductions were placed in the context of the long-term, natural hydrological disturbance history, to fully and more objectively understand the extent to which, for each river, short-term extreme flow reductions represented potentially more intense, physical pulse disturbances (Section 1.4.3) to the benthos than natural low flows (Humphries

and Baldwin 2003). Actual instantaneous discharges or magnitudes of reduction in flow were shown not to be particularly meaningful disturbance measures in themselves. Thought not specifically addressed here, the potential implications across sites of antecedent flow events (e.g. Ward 1976a; Biggs and Close 1989; Feminella and Resh 1990; Feminella 1996; Wood *et al.* 2000; Konrad *et al*. 2008), differences in high flow regimes, as well as the possibility of complex interactions between high flows and low flows as disturbances, are acknowledged (and examined to some extent in Section 8.7).

Comparison of observed summer discharges with historical flow records suggested that dry seasons of lower than usual flows were being experienced at the Elands and Molenaars sites during the study, more so than at other sites, as discussed further below. This factor might have had important implications with respect to the potential responses of invertebrate assemblages to flow disturbance during the field experiment. Although the biota might well be expected to be adapted to very low flows during the dry season, and hence, prepared to cope with unnaturally low flows at such a time, it is also likely that they are experiencing a period of natural, flow-induced stress (O'Keeffe *et al.* 2002).

In terms of natural patterns of instantaneous discharge recorded during the study, as anticipated, for all sites lowest discharges occurred from February to early March. In most instances, discharges were highest in December, except in the Riviersonderend reach where elevated flows from late April onwards reflected an earlier, more pronounced transition to autumn flow conditions at this event-responsive site. The Riviersonderend site exhibited the most variable short-term flow pattern, with a more than five-fold discharge amplitude, while the other sites exhibited a more limited range in low flow magnitude throughout the study period, in the order of a factor of two.

For all sites and months, instantaneous discharges were lower than the corresponding historical average daily discharge and higher than the absolute minima on record, but did not bear a dependable relationship with any particular low flow index for any site, even within the peak dry season. As mentioned previously, therefore, where relationships are being sought between low flows and biotic response, especially in the short-term and across different rivers, selection of appropriate low flow indices ought to be undertaken with due attention to natural trends in low flow variables over time. The results also suggested that the use of a single standard hydrological index (e.g. Q_{90}, Q_{95} or 7Q10) to characterize ecologically relevant low flows across all low flow months and among different sites, as done in many ecohydrological and environmental flow studies to date (Sections 1.5.3 and 1.4.2), might also be inappropriate. They thus support Smakhtin's (2001, p. 175) contention that "low flows should rather be viewed as a dynamic concept and not described by just one single low-flow characteristic."

Low-flow disturbance was quite high in the Elands River naturally, with instantaneous discharges spanning the lower range of flows in any month, in the order of or slightly higher than Q_{90} to Q_{95}, and approaching historical minima during April. For the Molenaars reach, measured natural discharges shifted from

percentage exceedences below Q_{75} to between Q7d-low and Q_{95} as summer progressed. In the peak of the dry season, natural discharges declined to marginally lower than the corresponding monthly Q_{95} discharge (in the order of Q_{96}, February, to Q_{87}, March). In contrast, in the same period, with an average diversion of 36% of total dry-season flow, discharges were effectively reduced to about the same as the absolute minima that the river had been exposed to naturally in the long term (Q_{99}-Q_{100}). Additionally, reinstatement of natural flows from April onwards represented an increase in discharge magnitude of *c*. 61% in the flow-impacted section, in contrast with a slight (2%) decrease in natural discharge. For the Du Toits site, natural discharges were moderate, fluctuating between Q_{30} and Q_{75} (Q_{56} and Q_{32} for February and March, respectively). About 86% of dry-season flow was abstracted from the Du Toits River upstream of the impact location, leaving only 14% of the total natural flow. The diversion resulted in flows markedly lower than even the absolute minima on historical record midsummer. An increase in flow magnitude of *c*. 440% was experienced in the impacted reach with the reinstatement of natural flows in April, in comparison with a natural Q_{inst} increase of only 8%. Natural discharges fluctuated most of all sites in the Riviersonderend reach (from just above Q7d-low to well above Q Median Median), without a consistent relationship with any particular hydrological index. As in the Du Toits reach, instantaneous discharges were fairly high when compared with historical figures and equivalent to Q_{68} and Q_{50} during February and March, respectively. Only marginally more flow was diverted experimentally from the Riviersonderend reach than the Du Toits reach, also rounding on average to *c.* 86%. The magnitude of the low flow disturbance was similarly extreme at the former site, to below the absolute minima recorded historically (also Q_{100} in both months). The Riviersonderend reach was subjected to the most dramatic discharge increase of all experimental reaches with reinstatement of natural flows, at about 1028%, which contrasted markedly with a natural flow increase of 130%. In all of the flow-impacted reaches, the unnatural flows were for similar durations of nearly two months (43 to 53 days) that extended in time well beyond any natural, very low flow spells on record.

4.5.3 Flow indices of potential ecological relevance for invertebrates

A subset of 16 of a wide range of 32 non-redundant flow variables analysed, were particularly influential in characterizing similarities and differences among river flow regimes in a way likely to support ecological inference (see also Section 8.7, in which the actual relevance of flow variables for invertebrates was evaluated). Although the various flow variables examined described different aspects of a river's flow regime and showed varying degrees of intercorrelation, as noted elsewhere (Hughes 1987; Hughes and James 1989; Jowett and Duncan 1990; Richards 1990; Smakhtin and Toulouse 1998; Growns and Marsh 2000; Olden and Poff 2003) many of them were significantly, if not always strongly, positively or negatively intercorrelated (cf. Poff (1996), for 806 U.S. diverse stream sites, where correlations among flow variables across all sites were generally low). Moreover, daily flow indices were not always correlated strongly with monthly or annual/inter-annual ones, as Olden and Poff (2003) also demonstrated, and revealed quite different aspects of flow regime character from them. This finding underscored the need to assess invertebrate response for various temporal windows of flow disturbance history.

Some 83% of the total variance in hydrological regime descriptors (derived from all study rivers), based on principal components analysis, could be attributed to the influences of events at both the high (flood) flow and dry-season low flow ends of the flow-disturbance continuum, enforcing the prevailing view that streamflow environments are more appropriately represented along axes representing various configurations of hydrological variability than as discrete units (Poff and Ward 1989; Feminella 1996). River flow regimes were effectively characterized by different clusters of flow variables reflecting mid-dry season flow variability and magnitude, and flood attributes, widely separated from a larger group of indices reflecting primarily the magnitude, as well as the predictability, of a suite of low flow measures. Of the wide array of low flow indices examined, seven were most clearly associated with regime characterization, reflecting the magnitude, variability and predictability of very low flows, particularly mid-dry season. The discharge equalled or exceeded 95% of the time (Q_{95}) and the mean annual minimum flow (MAM) were particularly important in distinguishing among the rivers. Also prominent were the coefficients of variation of annual minimum (CV_{QMin}) and dry season (CV_{Dry}) discharges, the median seven-day low flow, and two other low flow percentiles (Q_{80} and Q_{90}). All four of the high flow indices included, which encompassed attributes of flood magnitude, variability and frequency, also played a central role in representing river hydrological character. Key indices were the flow equalled or exceeded 5% of the time (Q_5) and an index of inter-annual variability of peak floods. The maximum annual discharge (Q_{Max}) and flood event of a 1: 2 year average return interval were also influential factors. In addition to mean daily discharge, variables representing overall regime variability and predictability, namely the annual coefficient of variation (CV), Colwell's predictability (*P*), and its components, flow constancy (*C*), contrasted with flow contingency (*M*), most usefully differentiated among site flow disturbance regimes. Plausibly, analysis using a more balanced or different set of flow attributes across general, high, and low flow groups, might have led to variously different groups of strongest influence on flow regime character, as also acknowledged by Clausen and Biggs (2000) for a similar characterization of the flow regimes of perennial New Zealand rivers.

Clausen and Biggs (2000) derived 35 variables of three main categories from daily flow data, to characterize the flow regimes of multiple perennial temperate New Zealand rivers. These were: (1) six variables describing general flow regime features (viz. CV, mean flow, Q_{50}, skewness, predictability and constancy); (2) 26 high flow variables, covering various aspects of event magnitude, frequency and duration; and (3) three low flow variables (viz. Q_{90} standardised by Q_{50} to represent regime flashiness rather than flow magnitude, the mean annual minimum, MAM, divided by Q_{50}, and a BFI). Four major flow groups could be delineated as a result, that reflected: river size (central tendency of magnitude); overall flow variability, including the magnitude of low and high flows; the volume of high flows; and the frequency of high flow events. In contrast with the high flow indices, all low flow indices exhibited a low degree of inter-annual variation. The Q_{90} and MAM grouped together, and with overall regime predictability and constancy, with which they were highly correlated. Both Q_{90} and MAM were identified as potentially influential to lotic biota, in terms of the degree of habitat loss associated with drying during low flows, but Clausen and Biggs (2000) considered the group of variables reflecting high flow frequency likely most influential in

constraining the biota. Importantly, for the perennial rivers in the present study, in addition to the two low flow indices singled out by Clausen and Biggs (2000), several attributes of the low flow regime reflecting aspects of the magnitude, variability, and predictability of naturally very low flows, were demonstrated to be potentially influential elements of the overall flow disturbance regime (see also Section 8.7). Consequently, the findings of this study firmly endorsed Clausen and Biggs' (2000) recommendation that a suite of flow variables containing at least one representative from each of the flow groups they identified be used in ecological studies, to ensure that the various facets of flow regimes are adequately addressed.

Although CV was only one of several key flow variables distinguished in the present study, in the hydrological characterization of 144 New Zealand river sites (Section 4.1), Biggs *et al.* (1990) found CV to be the best descriminator of river flow variability of several flow indices. Similarly, in Jowett and Duncan's (1990) hydrological characterization of 130 New Zealand rivers (Section 4.1) overall CV (CVFLOW) proved the best variable for separating sites, though the authors commented that other flow indices might be more pertinent for flood or biological studies (as supported in this thesis; Section 8.7). The index, CVFLOW, was examined in combination with the CVs of mean annual maximum and minimum flows, median and mean annual flow (MEANF), the means of annual maximum and minimum flows, as well as MEANF/catchment area and a baseflow index (BFI). As all variables except the CV of mean annual maximum flow were significantly intercorrelated, Jowett and Duncan (1990) concluded that it was not possible to single out any particular variable as most influential in describing regime type. The CVs of annual extremes (viz. CVs of mean annual maximum and minimum flows) were considered of limited utility, as they showed little relationship with other indices of flow variability. This finding is in contrast to the current study, as well as a number of others below, where indices of low flow variability derived for peak low flow periods (e.g. CVDry) complemented more general variability measures in site flow characterization.

Hughes and James (1989) were able to classify Victorian rivers, Australia, as possessing one of four characteristic low flow regimes based primarily on monthly flow duration index and CV of mean monthly minimum flows (PCA axis 1), and the CV of annual minimum flows (axis 2) (Section 4.1). Hughes (1987), in a hydrological regionalization of 77 Tasmanian rivers, found a significant correlation between the CV of monthly average low discharges and annual CV, showing that areas of Tasmania with higher coefficients of variation of annual flow tended to exhibit higher variability of monthly low flows. Hughes and Hannart (2003) found an index representing the sum of the average CVs for the three main dry months (similar to CVDry of this study) and wet season months useful for representing long-term flow variability, alongside a complementary measure of shorter term variability (a baseflow index, BFI). In combination as CV/BFI, the two indices represented an index of flow regime variability (CVB) that was far better differentiated than annual CV across the wide range of different South African flow regime types addressed. Poff (1996) successfully classified the flow regimes of a diverse 806 relatively undisturbed, small to medium-sized streams in the United States based on ten main flow indicators of flow variability and predictability for

average conditions (e.g. CV of daily flows, *P*), low-flow disturbance and high flow extremes. The low flow indices considered as disturbance measures were the seasonal predictability and timing of low flows, seasonal predictability of non low flow periods, a baseflow index, and the extent of intermittency.

It was similarly possible for the present study, using combinations of the key flow indices identified through varied analyses, to highlight the features of site flow regimes potentially most influential in invertebrate response to low flow disturbance. The distinctly different hydrological character of the Riviersonderend site as compared with the other sites was unquestionably of tremendous import in understanding variations in invertebrate response observed across sites (Chapters 7 and 8). When compared with the other study reaches, the flow character of the Riviersonderend River at the site was most influenced by the high variability and low predictability of its low flows mid-dry season, as well as the flashiness of its high flow regime. Although of fairly similar size and location, the Du Toits reach appeared to respond more gradually to peak flow events than the Riviersonderend site. It also exhibited the most stable, distinctive low flow regime (and hence, low-flow disturbance history), as well as lowest overall variability, of all study sites. The flow character of the control site, the Elands, appeared most strongly affected by quite predictable, high annual flow variability. In contrast, the Molenaars River exhibited a comparatively moderate disturbance history, likely indicative of its relatively high stream order and foothill location.

4.5.4 Concluding remarks

The majority of ecological studies of low-flow disturbance as yet do not include rigorous hydrological characterization, and there were remarkably few ecohydrological studies addressing low flows with which to compare findings. Equally, as Monk *et al*. (2006, p. 609) observed "Hydrological classification is now widespread (Hannah *et al.*, 2000; Snelder and Biggs, 2002) although the integration with ecological data is rare but an essential process for true hydroecological investigations (Hannah *et al.*, 2004)." Fully concurring with this viewpoint, as well as with that articulated by Poff and Allan (1995, p. 619) that the "hydrological regime alone cannot fully explain patterns in assemblage structure, because other important habitat features are known to have local influence independent of discharge", the extent to which low flows influenced invertebrate assemblage dynamics, directly or through changes in physical habitat, was investigated in subsequent thesis chapters.

It was without doubt essential, that natural and artificially induced extreme low flows were placed in the context of the long-term hydrological disturbance histories of individual study rivers. Despite numerous general similarities in flow regime, each river possessed detectably different, natural general and low flow signatures. Moreover, it was possible to identify a number of salient indices of flow variability, predictability, low flows, and also high flow events, that differentiated among site hydrological regimes and were therefore of potential ecological relevance in terms of characterizing invertebrate response to flow-related physical disturbance. Poff (1996, p. 87), in discussing the value of streamflow typing in effectively controlling for hydrological variation, so that the role of other environmental factors in structuring stream

assemblages might be discerned, emphasised that as many flow descriptors are based on long-term averages "residual variance in observed ecological patterns might be reduced by taking site-specific hydrological history into account. This should be more pronounced for ecological variables that fluctuate directly in response to hydrological disturbance (e.g. relative abundance...than for ecological variables that represent long-term adjustments to a regime of disturbance (e.g. species traits...)". As might be expected, therefore, delineation of rivers into groups of similar flow response type potentially increases the predictive capacity in developing relationships between flow variability and invertebrate assemblage response (Monk *et al*. 2006; Konrad *et al*. 2008) (see Chapters 8 and 9).

Comparison of recorded discharges with river flow histories was particularly effective in demonstrating that all experimental flow reductions (and subsequent flow recoveries), irrespective of their differences in magnitude, represented extreme low-flow events not experienced previously in any of the river reaches in either magnitude or duration over a known period of almost 30 years. Consequently, invertebrate assemblages of impacted locations were subjected to flow disturbances that qualified as potentially severe in effect, albeit single events and for short periods of time, crossing natural hydrological thresholds and at a time of natural flow stress (Lake 2003; Boulton 2003; Humphries and Baldwin 2003). The extent to which the benthos might be adjusted to such a disturbance regime over longer time frames remains unknown.

5. SHORT-TERM EFFECTS OF NATURAL AND UNNATURAL LOW FLOWS ON RIVER CHEMISTRY

5.1 INTRODUCTION AND APPROACH

The hydrological regime is recognized as affecting the ecological integrity of a river not only directly, but also indirectly through flow-mediated changes in various physical attributes and chemical constituents (hereafter referred to as water chemistry) (Section 1.2.2, Figure 1.1). Spatial and temporal variations in water chemistry, alongside the scales of hydrological variability with which they are intimately linked, are natural features of rivers (Armitage 1984; Jowett and Duncan 1990; Dallas and Day 1993; Grimm 1994; Williams 1996; Dallas *et al.* 1998; Lake 2000). Aquatic biotas are adapted to these natural spatiotemporal variations in water quality tied to river flow regimes (Bunn and Arthington 2002; Nilsson and Renöfält 2008). Flow-related changes in chemistry, often complex and difficult to predict quantitatively, can exert a wide range of potential stresses on riverine biota (Armitage 1984; Dallas *et al.* 1994; Williams 1996) which may become pronounced at very low flows (Nilsson and Renöfält 2008). In many cases, water quality deteriorates rapidly once flow reduction leads to flow cessation and habitat fragmentation, with accumulated water of poor quality no longer adequately diluted or exported from the reach (Boulton 2003; Lake 2003). In other instances, however, severe low flows, even for protracted periods, appear to have limited influence on chemistry (e.g. Wood and Petts 1994). In characterizing the reactions of benthic macroinvertebrates to natural and unnatural low flows in this study, cognisance needed to be taken of the possible effects of water quality change that might influence their responses, at least in the short-term (Sections 1.2.1 and 5.1.3).

Numerous texts on the effects of river regulation address the general, interlinked effects of altered hydrology on water quality and aquatic invertebrates (e.g. Ward and Stanford 1979, 1987; Armitage 1984; Armitage and Petts 1992; Dallas and Day 1993). A recent review of literature on the interrelationships among discharge, water quality and biotic response in rivers, with a synopsis of literature studies of the effects of increased discharge (including floods) on various physical and chemical variables, is provided in Malan and Day (2002b). Comparatively fewer studies have rigorously demonstrated the converse relationships between discharge reduction and chemistry, or have examined altered water chemistry as a contributor to invertebrate response to naturally or manipulated extreme low flows (Williams 1996; Caruso 2002; Malan and Day 2002b; Dewson *et al*. 2007a, c). Of these studies from which evidence of low flow effects on chemistry can be gleaned, most address drought conditions (Dahm *et al*. 2003) or are of temporary streams (e.g. Harrison 1966; Fisher and Grimm 1988; Boulton and Lake 1990). More often, it is simply assumed that flow-related changes in water chemistry bear an influence on invertebrate assemblages under low flow conditions.

5.1.1 Effects of discharge reduction on water chemistry

Factors such as season, antecedent rainfall and land use all have bearing on the instream concentrations of chemical constituents resulting from a given discharge, as do various others in the case of anthropogenically altered rivers in particular (Extence 1981; Armitage 1984; Chessman and Robinson 1987; Petts 1989; Britton *et al*. 1993; Allan 2004). Further, water quality variables are modified not only by the absolute quantity of flow, but also by the longitudinal and lateral distribution of physical characteristics of the river system, such as channel geometry, vegetation cover and hydraulic attributes (Grenney *et al.* 1976). With reduction in streamflow, the concentrations of physical and chemical variables change as a function of both instream (the focus of this chapter) and catchment processes (Malan and Day 2002b). Moreover, with river physical and chemical conditions often highly intercorrelated (e.g. Boulton and Lake 1990; Pollard *et al.* 1996; Chapter 2), there are commonly concurrent effects on physical habitat (Chapter 6) and water quality at low flows. For instance, changes in water quality with reduced discharge may occur in concert with riverbed desiccation. It is often difficult to differentiate among such interrelated effects of water quality and habitat on the biota (Malan and Day 2002b).

The complexities of relationships between chemistry and discharge, and the vast number of influential factors potentially implicated, have been reflected by various flow-concentration rating curves (Grenney *et al.* 1976; Malan and Day 2002b). Most characteristically, individual chemical constituents increase in concentration as discharge magnitude decreases (typically in linear or logarithmic fashion), with the converse effect occurring with increased dilution capacity at high flows, assuming all other factors affecting chemistry are constant (Covich *et al*. 1978; Malan and Day 2002a, b). Alternatively, the discharge-concentration (Q-C) relationship can show an initial concentration increase and then level off. Some constituents may show little or no relationship with discharge or the relationships may be inconsistent, especially where factors controlling instream concentrations are complex or numerous (Malan and Day 2002a). In most instances, variability is a common feature of the Q-C relationship (Jowett and Duncan 1990; Malan and Day 2002a, b). At different river sites, individual chemical constituents may show different relationships with discharge magnitude. Moreover, in terms of time series of flow change, relationships may be hysteretic in nature (Malan and Day 2002b). Such trends underscore the need to consider the effects of discharge dynamics on chemistry on a site-specific and variable by variable basis.

Low flows (including those due to droughts) are recognized as typically resulting in a deterioration in water quality that may be substantial (e.g. Larimore *et al.* 1959; Anderson and McCall 1968; Ladle and Bass 1981; Armitage 1984; Cowx *et al.* 1984; Chessman and Robinson 1987; Boulton and Lake 1990; Dallas and Day 1993; Chutter and Heath 1993; Weeks *et al.* 1996; Pollard *et al.* 1996; Williams 1996; Lake 2000). Such low flows directly influence all the inputs and outputs that are discharge dependent (e.g. dissolved and particulate organic matter; Lake 2000). Some longitudinal ecological processes become fragmented at very low flows, limiting the transport of resources such as nutrients (Lake 2000). Similarly, extreme low flows may affect lateral connections and/or processes, such as a deterioration of physicochemical conditions in dry

season refuges created as a result of the loss of lateral hydrological connectivity (e.g. Bunn and Arthington 2002). The influence of groundwater on surface-water chemistry is known to increase in some instances at very low flows, potentially introducing variations in local chemistry (Clinton *et al*. 1996; Rader and Belish 1999; Caruso 2002; Dahm *et al.* 2003).

Effects of reduced discharge on specific water quality constituents

While naturally spatiotemporally variable at low flows, water temperature generally has been assumed or found to increase, or show greater extremes (Larimore *et al*. 1959; Hynes 1970; Ward 1976), with decreasing discharge and water volume (and associated declines in current velocity and water depth), as well as with increases in dry-season air temperature and solar radiation (Grenney *et al.* 1976; Williams 1996; Malan and Day 2002b; Lake 2003). Small streams especially, can become particularly vulnerable to temperature fluctuations under very low flows (Nilsson and Renöfält 2008). Increased temperatures at low flows may elevate primary production (e.g. proliferation of algae) and enhance invertebrate production (e.g. Extence 1981) leading to various secondary effects (Nilsson and Renöfält 2008).

Increases in temperature with decreasing discharge have been commonly reported (e.g. Stehr and Branson 1938; Larimore *et al*. 1959; Extence 1981; Ladle and Bass 1981; Cowx *et al*. 1984; McElravy *et al.* 1989; Jowett and Duncan 1990; Petts and Bickerton 1994; Pollard *et al.* 1996; Dallas 1998; Cazaubon and Giudicelli 1999; Rader and Belish 1999; Caruso 2002; Dewson *et al*. 2007b). Highest temperatures in least impacted rivers in the Western Cape occurred in summer, at the lowest recorded discharges (Dallas 1998). Natural changes that occurred during the summer dry season in northern California rivers, with gradual flow reduction to the point where smaller streams became intermittent, included increases in water temperatures and their diel ranges (as well as silt and detritus accumulation) (McElravy *et al.* 1989). With late summer flow cessation, due to summer drought, water temperatures markedly increased in a small, perennial chalk Stream, U.K. (Ladle and Bass 1981). In examining the spatiotemporal effects of prolonged extreme low flows during summer (the result of a severe two-year drought) at 12 river sites across the Otago Region, South Island, New Zealand, Caruso (2002) found that the overall trend in water temperature across most sites was one of an increase in magnitude and for longer periods than usual. Substantial temperature increases were observed at extreme low flows in the most affected part of the region (with dissolved oxygen concentrations tending to decrease in concert, but generally remaining suitable for aquatic biota). Cazaubon and Giudicelli (1999) reported an increase in daily and annual thermal variation as one of the major consequences of year-round reduction in flow to $1/70^{th}$ of average annual discharge, in the large Durance River, France. Lillehammer and Saltveit (1984b) reported only a small increase in water temperature midsummer from that established pre-regulation (but no significant changes in pH or conductivity), with reduced summer discharges, and less pronounced in the upper reaches, in the regulated River Suldalslågen, western Norway. Water temperature was significantly lower under natural low flows, however, than downstream of a diversion removing 98% dry season flow, in a tropical Hawaiian river (McIntosh *et al*. 2008).

Decreases, variable, or no responses in temperature have also been reported with natural and artificial flow reduction (Dewson *et al*. 2007c). Moreover, significant positive correlations were found by Jowett and Duncan (1990), between flow variability and mean annual water temperature, annual temperature variation, and average summer temperature, for groups of New Zealand rivers. Experimental discharge reduction by 90% for an abnormally long period of three-months did not result in a measurable temperature difference between control and experimental stream sections in Blacktail Creek, U.S.A. (Kraft 1972). According to Dewson *et al*. 2007b; Section 5.3), dramatic experimental diversions in multiple New Zealand streams generated increases, decreases or no obvious responses in temperature. Caruso (2002) noted that water temperatures can be reduced at low flows in some cases, as a result of cooler underflow and groundwater inputs through the streambed (representing key thermal refuges for aquatic biota). A year of severe drought in a perennial Colorado mountain stream, that resulted in low flows for two months and negligible flow (and drying in the lower section) for a further two months, followed by a year of natural flows, did not result in detectable differences in water temperatures over that time, because of a major influence of groundwater in the alluvial stream segment (Canton *et al*. 1984).

Reduced dissolved oxygen (DO) concentrations and elevated biochemical oxygen demand (BOD) are expected in summer and during extended periods of low flow, particularly due to lower saturation concentrations with increasing insolation and temperatures (Anderson and McCall 1968; Dallas and Day 1993; Williams 1996; Covich *et al*. 2003). Natural variability in oxygen levels at seasonal to within-daily scales also may be attributed to factors such as gas exchange and photosynthetic oxygen production or respiration depletion (Williams 1996; Caruso 2002), as well as changes in current velocity (Gordon *et al.* 1992), water depth (Williams 1996; Davies and Day 1998) and pool surface area to volume ratios (Malan and Day 2002b). With marked discharge reduction, particularly when commensurate with high water temperatures, DO concentrations in biotopes such as standing-water pools might reach critically low to hypoxic levels for aquatic biota (Malan and Day 2002b).

While there appears variable and rather limited evidence that flow reduction leads to changes in DO concentrations (e.g. Rader and Belish 1999; Cazaubon and Giudicelli 1999; Caruso 2002; Dewson *et al*. 2007a), Dewson *et al*. (2007c) noted that measurements tend to be diurnal, with DO minima at night seldom ascertained. Some studies have associated increases in oxygen concentrations with extremely low flows, with increased algal densities cited as a key contributing factor (e.g. Pollard *et al.* 1996; Ruse and Davison 2000; Section 5.3). In intermittent streams, poorer water quality, including lower DO levels, has been reported from pools during seasonal, extreme low flows (e.g. Pires *et al*. 2000). Monthly DO showed different degrees of decline for New Jersey, U.S., rivers during abnormally low flows due to five years of drought (Anderson and McCall 1968). While declines in %DO concentrations were clearly apparent in the Passaic and Raritan rivers, levels were relatively constant in the Toms River until detritus was flushed from the system during a period of higher flows, when they decreased.

Increases in electrical conductivity (EC), total dissolved solids (TDS), and the concentrations of constituent ions, have been reported as common trends with discharge reduction (e.g. Anderson and McCall 1968; Pollard *et al.* 1996; Rader and Belish 1999; Malan and Day 2002b; Caruso 2002; Dewson *et al*. 2003; see also Section 5.3). Few studies have demonstrated a lack of response or a decrease in EC particularly, at low flows (Dewson *et al*. 2007c), although Dewson *et al*. (2007a, b) and James *et al*. (2008) showed little response in EC to experimentally induced discharge reductions (Section 5.3).

The highest recorded TDS values in the Sabie-Sand River system, South Africa, occurred in the Sand River during zero-flow conditions due to drought (Weeks *et al*. 1996). In the perennial Waterston Stream, U.K., potassium concentrations increased with flow cessation and streambed desiccation due to summer drought (Ladle and Bass 1981). In an analysis conducted for nine New Zealand rivers, however, mixed correlations were found for flow and chloride (Biggs and Close 1989). No significant flow-related differences in total dissolved solids were found between a Hawaiian stream reach at natural dry season flow and the downstream reach subjected to approx. 98% flow reduction (McIntosh *et al*. 2008). In terms of relationships between water chemistry and groupings of rivers based on flow variability, Jowett and Duncan (1990) found that conductivity decreased as flow variability decreased.

Decreases in pH with increasing discharge has been observed in several studies (Malan and Day 2002b), which suggests that the converse may hold at low flows. However, variable responses to natural and artificially reduced low flows have been reported for pH (Dewson *et al*. 2007c). Williams and Hynes (1977) reported high pH levels in pools with abundant algae in temporary streams during summer. Increased pH values at extremely low discharges also were reported in the South African Sabie and Sand rivers, perennial and increasingly temporary systems, respectively, by Pollard *et al.* (1996). In contrast, decreases in pH occurred with manipulated dry-season flow diversions in studies by McIntosh *et al*. (2002, 2008). Comparison of water quality in a perennial Hawaiian stream reach (Iao Stream) impacted by 92-97% summer discharge reduction with that at natural low flows above the water withdrawal point, showed significantly higher pH in the latter site (McIntosh *et al*. 2002). Similarly, significantly higher pH values were recorded at natural low flows, as compared with values in a downstream reach of the tropical, perennial Waihee River, Hawaii, impacted by roughly 98% flow reduction (McIntosh *et al*. 2008). Stream pH was generally unaffected by experimental flow diversions in three New Zealand streams, with a maximum decline of 12% in Kiriwhakapapa Stream, where the proportion of flow diverted was the lowest of all but still exceeded 89% (Dewson *et al*. 2007a, b; Death *et al.* 2009). In Booth's Creek, with extension of the period of impact to two months, pH decreased significantly (James *et al.* 2009). No change in pH occurred with mild to severe flow diversions across three small, U.S. perennial mountain streams (Rader and Belish 1999). Jowett and Duncan (1990) found no significant general relationships between river flow variability and pH.

The few studies of low flow effects on nutrient dynamics and decomposition, as well as metabolism of the products of biochemical processes occurring during extreme low flows following reinstatement of normal flows (Lake 2003), illustrate their complexity and how variable flow-nutrient patterns can be in different contexts (e.g. Cuffney and Wallace 1989). Flow cessation terminates the transport of nutrients and detritus in surface flow (Lake 2003). Dewson *et al*. (2007c), in a review of the effects of decreased streamflow on nutrient concentrations in small perennial streams, found a few supporting studies for increases or no response in nutrient levels, but decreases in nutrient concentrations were more commonly reported.

Increases or decreases in nitrate levels have been recorded with stream discharge (see references in Chessman and Robinson 1987), and levels may fluctuate quite widely over the year (e.g. Britton *et al*. 1993). Malan and Day (2002b) reported that nitrates naturally often showed a positive correlation with discharge, with a distinct increase often occurring after rainfall broke a dry spell. Extended periods of very low flows are assumed to likely lead to longer residence times of accumulated, elevated nutrients (as well as any system toxins) (Covich *et al*. 2003). In the Sabie-Sand River system, South Africa, concentrations of nitrates and ammonia remained stable or more commonly slowly increased over time, from commencement of a severe drought, reaching high levels in the final phase of pool isolation (Pollard *et al.* 1996). Increased levels of ammonia also were reported at low flows by Anderson and McCall (1968). Brooker and Johnson (1984, cited in Malan and Day 2002b), however, found lowest nitrate (and highest phosphate) concentrations at summer low flows in 12 Welsh streams. Both positive and negative relationships between mean daily flow and nitrate-N (NO_3-N) were found for the nine New Zealand gravel-bed rivers (Biggs and Close 1989). For eight of the nine rivers studied, correlation analysis between mean daily discharge and water quality showed that total Kjeldahl nitrogen (TKN), ammonia-N (NH_4-N), dissolved reactive phosphorus and total phosphorus were highly significantly positively correlated with average daily discharge. In an analysis of relationships between water chemistry and groupings of rivers on the basis of flow variability, no significant relationships were found by Jowett and Duncan (1990) for flow variability and inorganic nitrogen or dissolved phosphorus, but total Kjedahl nitrogen decreased as flow variability decreased.

Relationships between phosphorus and discharge also tend to vary, though phosphate concentrations may be naturally fairly constant in nutrient-poor systems (Malan and Day 2002b). Phosphorus dynamics may be affected by changes in other chemical constituents or in physical habitat hydraulics. For example, changes in pH and conductivity with altered flows can affect the proportion of dissolved or bound phosphorus (Malan and Day 2002b). Meyer (1980, cited in Pringle *et al*. 1988) recorded significant differences in phosphorus dynamics between pools and rapids.

Dissolved phosphate concentrations dramatically increased in response to decreasing discharge and evaporation, and were also high immediately after flow resumed, as a perennial chalk stream (subjected to natural flow cessation only in very dry years and effectively perennial for some years prior), Waterston Stream, U.K., ceased to flow and dried up due to summer drought (Ladle and Bass 1981). Nitrate

concentrations also increased above baseline levels, though to a lesser extent (but cf. a subsequent more prolonged drought in 1974, where nitrates reached maxima), with flow reduction and once flow resumed (Ladle and Bass 1981). Houston and Brooker (1981, cited in Malan and Day 2002b) reported elevated phosphate levels at minimum discharges, during summer, in two Welsh streams. In the severe drought experienced by the Sabie-Sand River system, Pollard *et al.* (1996) observed that, as for nitrates above, figures for soluble reactive phosphate generally increased as flow reduced and river pools became increasing isolated, but remained low overall. Caruso (2002) found significantly lower median total phosphorus (TP) concentrations at severe drought flows than under natural low flow regimes for an aggregated set of 12 river sites, New Zealand. Total phosphorus figures for the most flow-impacted part of the study area (North Otago) showed somewhat variable responses to reduced discharge, remaining low, relatively constant, or more typically declining during the drought period; in all instances, concentrations were lower than the recommended national guideline for aquatic ecosystems of 0.1 mg ℓ^{-1}. Similarly, total nitrogen (TN) values for stream sites were low, constant or decreased with extreme discharge reduction, and below those considered suitable for lotic ecosystems (0.75 mg ℓ^{-1}). Prairie and Kalff (1998a, cited in Malan and Day 2002b), in a study of seven Canadian headwater streams, found that increasing discharge resulted in decreases, increases or no effect on dissolved phosphate concentrations.

Increased retention and accumulation of settled-out fine sediments (Dallas *et al*. 1998; Davies *et al*. 2000) dissolved and particulate organic matter (Cuffney and Wallace 1989), as well as decreases in suspended sediments (Anderson and McCall 1968; Chessman and Robinson 1987; Caruso 2002), are common consequences of reduced flows or flow cessation (Malan and Day 2002b; Lake 2003) attributed largely to declines in transport velocities (Dewson *et al*. 2007c). Supporting studies include those of Kraft (1972), Wright and Berrie (1987), Cuffney and Wallace (1989), Bickerton *et al*. (1993), Wood and Petts (1994), Castella *et al*. (1995), Everard (1996), Englund and Malmqvist (1996), and Dewson *et al*. (2007a).

Increased fine sediment cover with enhanced accumulation of sediments was reported in two (more anthropogenically altered) of three New Zealand streams subjected to prolonged artificially reduced flows, while the most pristine stream showed no distinct response (Dewson *et al*. 2007a; James *et al.* 2009). Caruso (2002) reported decreases in sediment and turbidity with reduced dilution at extreme low flows, as well as significant increases in bacterial contamination (faecal coliforms), in variously anthropogenically affected streams in New Zealand. Decreases in suspended sediments and turbidity (and in DO, as well as increases in dissolved solids, BOD and coliform bacteria) were reported with a protracted five-year drought for four rivers in the U.S.A. (Anderson and McCall 1968). Biggs and Close (1989) found a significant positive correlation between total suspended solids and flow for eight of nine New Zealand rivers. Conversely, turbidity increased with shrinking pool size in pools of the Sabie and Sand rivers that persisted during protracted low flows (Pollard *et al.* 1996). Short-term experimental flow reduction to extreme levels in three small New Zealand streams generally resulted in small or inconsistent responses in functional measures such

as leaf breakdown and primary productivity (periphyton), while retention of coarse particulate organic matter was most responsive in showing an increase with decreased discharge (Death *et al*. 2009).

5.1.2 Invertebrate responses to flow induced changes in water chemistry

Lotic invertebrates are influenced in various ways by different water quality variables (Dallas *et al*. 1994; Williams 1996 p. 636, Figure 1) and limited to specific ranges of physical environments by their differing physiological tolerances to chemistry (King 1981; McAuliffe 1983). For instance, a number of Chironomidae species can tolerate a daily drop in oxygen, but not a prolonged period of low oxygen levels (O'Keeffe and Dickens 2000). Invertebrates may therefore be expected to exhibit varying responses in terms of assemblage composition or distribution, or particular biological attributes, in relation to flow-related alterations in water chemistry, including those brought about by changes in physical habitat (Lake 2000; see Section 6.1, Figure 6.1) (in addition to responses to flow *per se* - Section 7.1).

Invertebrate responses to flow conditions may be predicated on ambient water quality conditions and the resultant makeup and attributes of the assemblage. For instance, Dewson *et al*. (2007a) and Death *et al*. (2009) postulated that the impacts of whole-stream experimental diversion by more than 89% on the structural integrity of invertebrate assemblages varied among three small New Zealand streams, because of differences in the sensitivity of the assemblages to stream varying water quality, from pristine to moderately anthropogenically impaired (Chapter 7). Also, Castella *et al*. (1995) and Suren *et al*. (2003) demonstrated distinct differences in the responses of invertebrate assemblages to very low flows (including due to abstraction) dependent on river nutrient status. Abnormally low dry-season flows and partial bed exposure, due to a severe drought over two years in the anthropogenically impacted, lower LaTrobe River, Australia (Chessman and Robinson 1987), led to a noticeable deterioration in water quality. While decreases in [DO] and marked increases in conductivities occurred, effects on invertebrate richness and composition were limited (Section 7.1). However, the leptocerid, *Triplectides similis*, known to be intolerant of low oxygen concentrations, disappeared. Chessman and Robinson (1987) speculated that the general lack of a faunal response to extreme flow reduction indicated the restriction, even prior to the drought, of the species comprising the invertebrate assemblage to those generally tolerant of low DO. Wood *et al*. (1999) showed that water quality scores, for three biotic indices pertaining to invertebrate tolerances for water quality conditions, appeared related to the degree of flow stress experienced by three U.K. rivers, two of which were experiencing flow deficits, the Little Stour River (-31%, due to severe drought low flows and groundwater overabstraction) and the River Gadder (-24% deficit, due to water abstraction); the other site, Mill Stream, was in flow surplus with regulation. In a similar assessment, Davies *et al*. (2000) concluded that poor water quality associated with prolonged low flows during a drought in the Upper Murrumbidgee River catchment, Australia, may have resulted in the observed impaired biological condition at Australian River Assessment System (AUSRIVAS) reference sites.

At fine scales, such as biotopes or microhabitats, flow-related changes in water quality are known to affect invertebrate composition and distribution patterns. For instance, DO concentrations, influenced by flow hydraulics have been reported to directly influence the microdistribution of benthic insects (e.g. Armitage 1984; Williams 1996). For some taxa (e.g. Plecoptera), high current speeds with low oxygen levels result in fewer mortalities than low current speeds with the same oxygen levels (O'Keeffe and Dickens 2000). Invertebrates may also avoid flow-induced unacceptable water quality conditions through their behaviour. Lancaster and Hildrew (1993a) speculated that while two stonefly species (*Leuctra nigra* and *Nemurella pictetii*) in Broadstone Stream, England, had been shown to aggregate in low velocity patches in winter to avoid high flows (Section 7.8), they avoided such areas in summer because of local anoxia. Some mayflies, if unable to satisfy oxygen requirements by gill movements or positioning, emigrate by active drift entry (O'Keeffe and Dickens 2000).

Increasing emphasis is being given to experimental tests of the tolerances of indigenous riverine biota to chemical conditions associated with flow regime change, particularly in relation to establishing the environmental flow requirements of lotic taxa and specifying appropriate water quality ranges. For example, tests of the salinity tolerance of the mayfly, *Tricorythus* sp., of the South African Sabie River, showed that mortality was linked not only to conductivity levels associated with different discharges, but also to the nature of the salts implicated (Goetsch and Palmer 1997). Such ecotoxicological studies have been increasingly used to derive constituent-stress time series for various taxa, which can then be linked with time series from flow-concentration modelling (e.g. Malan and Day 2002a) to integrate water quality into environmental flow recommendations (Section 1.5).

5.1.3 Approach and objectives

It was not anticipated that there would be major changes in water chemistry associated with low flows, specifically the artificial flow reductions below natural magnitudes for extended durations, given the short-term and localised nature of the study. It was necessary, however, as one of the principal thesis objectives (objective 2, Section 1.2.1, Figure 1.2) to identify any potential secondary effects of flow reduction on water chemistry that might in part be influencing invertebrate response to extreme low flows. The extent to which any such effects might have bearing on the characterization of ecologically-relevant low flows for invertebrates could then be assessed (Chapter 8). A number of secondary objectives were pursued in this regard, to:

1. Establish the extent of variability in a range of physical properties and chemical variables over the low flow period, with particular reference to peak low flow months, at multiple sites.
2. Ascertain the extent to which there were changes in water quality under natural and manipulated extreme low-flows across and within sites.
3. Establish discharge-concentration relationships, so as to identify any general trends in individual chemical variables with flow reduction. A related objective was to identify any additional factors (e.g. biotope type, algal presence) that might further contribute to the nature of low flow-chemistry

relationships or their extent of potential influence on invertebrates.

4. Evaluate the extent to which short-term physicochemical conditions due to manipulated discharge reductions diverged from established historical patterns of natural water quality.

The methods for collection and analysis of water chemistry data are provided in Section 3.3. In Section 5.2 the results are presented in terms of observed trends in water chemistry, and related biophysical factors, associated with natural and unnatural reductions in river discharge. In Section 5.3, the implications of the findings are discussed, specifically in relation to characterizing low flows for invertebrates.

5.2 SHORT-TERM EFFECTS OF LOW FLOW CONDITIONS ON WATER CHEMISTRY

5.2.1 Spatiotemporal variations in chemistry, with particular reference to extreme low flows

Summary statistics reflecting the spatial and temporal variability in water chemistry variables at each site and location are given in Table 5.1. Corresponding time series plots are presented in Appendix 5.1 or, where particularly noteworthy trends were apparent, below. Direct comparisons of variable concentrations of individual variables at natural and abnormally low discharges also were made for the impact phase, where the resultant percentage differences in mean values provided an indication of the potential degree and direction of any flow-induced change from natural (Table 5.1). Pairwise statistical comparisons of data for control and impact locations for each site (Table 5.2) and among-site comparisons (Table 5.3) provided additional evidence of the extent to which there were natural inter- and intra-site differences in chemistry, as well as of potential effects of unnaturally low flows.

Conductivity and major ions

The time series of changes in conductivity at each site and location, for the duration of the low-flow study, is illustrated in Figure 5.1, while similar plots for cations and anions are given in Appendix 5.1a-f. Highly significant natural differences in EC (Figure 5.1) were found among sites over the study duration ($F_{3, 44}$ = 15.230, $P << 0.001$), although there were no within-reach differences at any site (Table 5.2). Lowest conductivities were recorded for the Elands River ($\bar{x}$ = 2.14 ± 0.22 mS m^{-1}), which was distinct from the other sites (Tukey HSD test; Table 5.2). Somewhat higher values were obtained for the Molenaars, Du Toits and Riviersonderend sites, with a maximum of 4.13 mS m^{-1} in the last river (Table 5.1). Typically, conductivities were similarly low and stable throughout the dry season at individual sites (Table 5.1), with maxima in the months of lowest discharges and subsequent decreases with natural flow increases in early autumn (Figures 5.1 and 4.7). Natural variability was lowest for the Elands site and greatest for the Riviersonderend reach representing an effective doubling in CV from 10 to 20%, respectively.

Percentage differences between flowing-water conductivities at natural and unnatural low flows were small (a maximum increase of 12%, and for the control site; Table 5.1), suggesting little change in conductivity with extreme low flow magnitudes and durations (but see below for post-impact effects). There was no apparent effect of a 36% discharge reduction on [EC] at the Molenaars site (Table 5.1). Similarly, at the Du Toits site, there was no apparent effect of an 85% or more reduction in discharge (well below the recorded absolute, natural minimum - Figure 4.9c), with maxima for control and impact locations comparably elevated in the month of lowest flow (February), at 3.88 mS m^{-1} and 3.67 mS m^{-1}, respectively. The Riviersonderend was the only experimental site that showed an appreciable increase in conductivity with unnaturally low flows (diverted to below the absolute recorded minimum - Figure 4.9d), in the still-flowing section of the mainstream and, to a greater extent, in isolated pools (Figure 5.1). In the latter patches, conductivities were up to 112% above already-elevated mainstream values, reaching an absolute maximum of 7.15 mS m^{-1} in March (Figure 5.1). Conductivities recorded from isolated pools of standing water at the other sites did not show any consistent increases or decreases in conductivity exceeding 10% of mainstream values, however, at natural or experimentally manipulated low flows (Figure 5.1). Discharge-concentration trends lent support to these varied results, pointing to more pronounced EC increases with flow reduction than in evidence from site time series (Section 5.2.2).

Importantly, for the Riviersonderend, the greatest divergence in conductivities between control and impact locations was not during the flow reduction phase, but following reinstatement of natural flows (Figure 5.1 and Table 5.1). Conductivity was measured 19 days after the increase to natural flow levels for the impact location (on 22 April 1995), while control data were collected earlier (8 April 1995). It is probable that the impact location was being subjected to even higher conductivities earlier on in the post-impact phase, immediately after the temporary diversion weir was dismantled (3 April 1995). Conductivities in the impacted location were elevated to 5.05 mS m^{-1} in April, a difference from overall minimum to maximum concentration of 105%, in contrast with a 4.13 mS m^{-1} May maximum under natural conditions and overall 62% range in concentration. The observed peak in conductivity in the impacted location was most likely a function of flushing of lower quality water, from the large area comprising slow/non-flowing biotopes and areas of the bed where connectivity with flowing areas of the channel had been lost (reported in Chapter 6). Recovery from residual effects of abnormal flows on conductivity was apparent a further 12 days later, with natural increases in May discharge (Figure 4.7), a total period until full recovery to natural levels of 31 days.

Changes in the concentrations of major ions at each site and location with low flow regime (Appendix 5.1a-f) were not necessarily in concert with conductivity (Figure 5.1) or one another. Comparisons between site locations yielded a significant difference for only Ca^{2+} ($U = 3.0$, $P = 0.015$), for the Du Toits site (control $\bar{x}$ = 0.020 mmol ℓ^{-1} vs. impact $\bar{x}$ = 0.011 mmol ℓ^{-1}) (Table 5.2). This difference could be attributed to natural variability (and not flow diversion) as the major divergence between locations was in the months either side of the impact phase, during which there was actually greatest correspondence in [Ca^{2+}] (Appendix 5.1d). At a site-specific scale, highly significant ($F_{3, 44}$ = 78.198-10.747, $P < 0.001$) or significant (for SO_4^{2-}; $F_{3, 44}$ =

3.729, $P = 0.018$) differences were found for all ions except Ca^{2+} ($F_{3, 44} = 2.252$, $P = 0.096$). In the last instance, differences in means among sites were small, in conjunction with naturally high levels of variability (CV = 31-67%, second only to silicon; Table 5.1). Tukey HSD results indicated the generally distinct site subgroups for the various ions (Table 5.3).

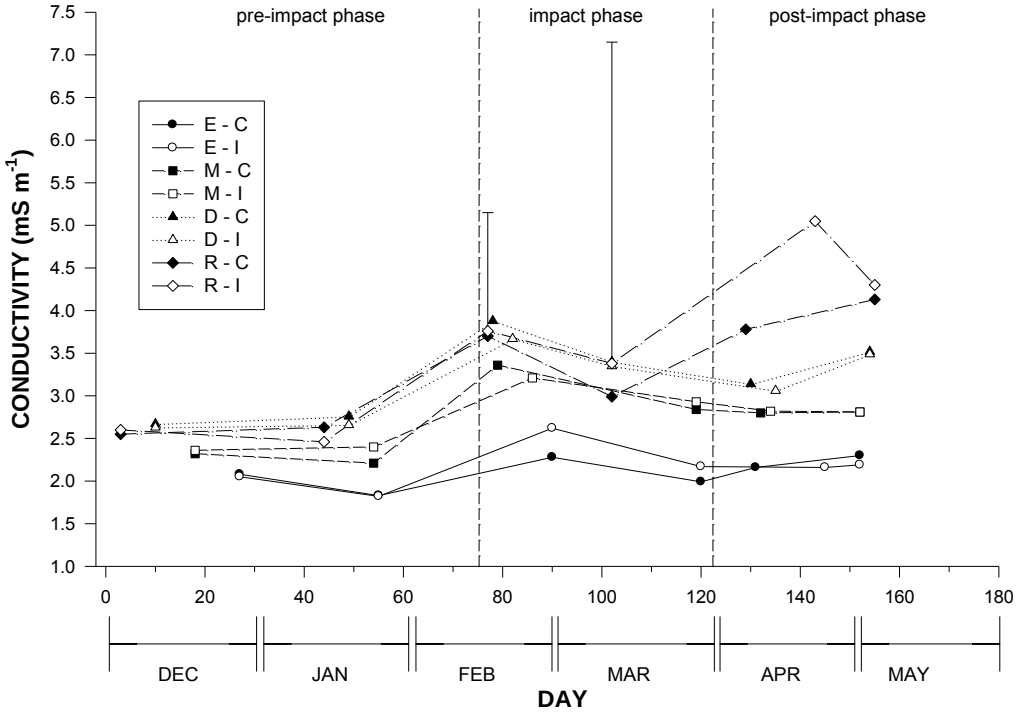


Figure 5.1 Changes in conductivity (mS m^{-1}) at the sites during the different phases of the low flow study. Demarcation of the impact phase is approximate. Upper error bars indicate conductivities in isolated standing pools, where values were ≥ 10% of mainstream EC. E = Elands; M = Molenaars; D = Du Toits; R = Riviersonderend; C = control; I = impact.

From Table 5.1 and Appendix 5.1a, it is evident that concentrations of the dominant cation, Na^+, fluctuated most spatially and over time in the Elands reach, with both the overall maximum of 0.206 mmol ℓ^{-1} (Feb) and minimum of 0.103 mmol ℓ^{-1} (Jan) recorded at this site, as well as a relative difference of 19% between locations in Feb-Mar. Generally, Na^+ appeared to be a fairly conservative variable from month-to-month, with little seasonal relationship with discharge. Furthermore, there was no apparent effect of unnaturally low flows on this variable, as borne out by Q-C trends below.

Over the study period, natural [K^+] was least variable at the Molenaars site and most variable in the Riviersonderend River, with CVs of 11% and 39%, respectively (Table 5.1 and Appendix 5.1c). Potassium concentrations for the group comprising the Du Toits and Riviersonderend sites (Tukey HDS results, Table 5.3) were roughly an order of magnitude lower (min = 0.002 mmol ℓ^{-1}, Jan, to max = 0.006 mmol ℓ^{-1}, May)

than those of the Elands and Molenaars (min = 0.006 mmol ℓ^{-1}, Feb, to max = 0.016 mmol ℓ^{-1}, Mar) (Table 5.1). The former group showed a gradual increase in K^+ from December to May, while values for the latter sites decreased after the peak of the dry season. Percentage differences in mean values for K^+ between the two locations during February-March were low for the control site and the Molenaars (with 36% flow reduction). A moderate 17% increase was found for the Du Toits impact location, due to a higher than natural [K^+] in February, suggesting a slight effect of flow reduction to below historical discharge minima. For the Riviersonderend site, the [K^+] time series showed no definite alteration from natural, although concentrations in the flow-impacted location exceeded background levels (Appendix 5.1b). The 37% increase in K^+ from mean natural values during February-March (Table 5.1) pointed to a possible effect of an approx. 86% reduction in low flows (as do Q-C trends).

Natural [Mg^{2+}] concentrations were low in all four rivers ($\bar{x}$ = 0.029-0.046 mmol ℓ^{-1}, overall range = 0.022-0.060 mmol ℓ^{-1}), and stable (similar, low CVs of 14-22%) under the natural low flow regime (Table 5.1 and Appendix 5.1c). One-way ANOVA results indicated two site groupings, with the Molenaars and Elands reaches showing significantly lower Mg^{2+}concentrations than the other two sites (Table 5.3). Flow reduction below natural levels did not appear to alter [Mg^{2+}] in most instances. However, during the impact phase, [Mg^{2+}] in the flow-impacted Riviersonderend location increasingly diverged from control values, reaching a 38% lower concentration in March (0.035 mmol ℓ^{-1} versus control = 0.056 mmol ℓ^{-1}). Later, after reinstatement of natural flows, the pattern was reversed.

Despite the abovementioned variability, natural mean Ca^{2+} concentrations were still similar among sites, ranging from 0.016 mmol ℓ^{-1} for the Riviersonderend, to 0.022 mmol ℓ^{-1} for the Molenaars (Table 5.1 and Appendix 5.1d). Comparisons of percentage differences in mean Ca^{2+} concentrations for the lowest flow period highlighted possible effects of unnaturally low flows for two sites, although the relatively high degree of variability tended to obscure patterns in the time series for all sites. For the Du Toits site, there were no obvious changes in Ca^{2+} with flow reduction. Although natural variability attained a maximum for the Molenaars site (CV = 67%), there still appeared to be an increase in [Ca^{2+}] in the impact location relative to the control location, of 45%, for the duration of the impact phase. Within the Riviersonderend site, an opposite effect of extreme low flows was found, with a 41% decrease in [Ca^{2+}] in the impacted reach during Feb-Mar (Table 5.1). Although the effects of flow reduction to below natural absolute minima (Figures 4.9b and 4.9d) could not be entirely discounted, Q-C trends did not support these results (Table 5.4).

Table 5.1 **Means (± SD), CVs (%), minima and maxima for water chemistry variables at natural low flows, as well as relative differences (%) between natural and unnatural, upper and lower values for the impact phase.** Natural values based on monthly data collected at both locations for the Elands (*n* = 12), and at control locations for the Molenaars, Du Toits and Riviersonderend sites (*n* = 6 each). ↑ represents a mean increase in a variable at unnaturally low flows, as compared with the control state during the same low flow period (Feb-Mar), while ↓ represents the converse trend. n/a – not appropriate. Variable units and abbreviations: conductivity (mS m^{-1}); pH (units); alkalinity ($HCO3^-$, mEq ℓ^{-1}); anions and cations (mmol ℓ^{-1}); nutrients (μmol ℓ^{-1}); biotope O_2 (% saturation); and minimum, maximum and instantaneous (Instant) temperature range (°C).

SITE AND CHEMICAL VARIABLE	NATURAL TEMPORAL RANGE (Dec-May) MEAN (± SD)	CV	MIN	MAX	IMPACT VERSUS CONTROL LOCATION % DIFFERENCE IN MEAN VALUES (Feb-Mar)
ELANDS					
Conductivity	2.14 (± 0.22)	10	1.82	2.62	↑ 12
pH	5.55 (± 0.40)	7	4.60	6.03	↓ 7
Alkalinity	0.065 (± 0.026)	40	0.036	0.121	↓ 8
Na^+	0.131 (± 0.028)	22	0.103	0.206	↓ 19
K^+	0.009 (± 0.003)	36	0.006	0.016	↓ 11
Mg^{2+}	0.032 (± 0.006)	19	0.025	0.047	↓ 14
Ca^{2+}	0.018 (± 0.008)	46	0.002	0.033	↓ 11
$C\ell^-$	0.115 (± 0.023)	20	0.065	0.147	↓ 8
$SO4^{2-}$	0.019 (± 0.006)	30	0.010	0.032	0
PO_4-P	1.604 (± 0.408)	25	0.908	2.365	↓ 23
NO_3-N	14.751 (± 3.124)	21	6.043	18.001	↑ 2
NO_2-N	0.108 (± 0.034)	31	0.050	0.167	↑ 8
SiO_2-Si	15.113 (± 18.516)	123	2.633	55.872	↓ 63
Riffle O_2	97.3 (± 3.9)	4	92.3	103.1	↑ 1
Run O_2	87.2 (± 6.1)	7	74.0	94.5	↓ 6
Pool O_2	62.1 (± 13.3)	21	38.6	80.3	↓ 32
Min Temp	14.6 (± 2.7)	n/a	9.9	17.5	↓ 2
Max Temp	22.1 (± 4.8)	n/a	15.1	27.2	0
Instant Temp	18.2 (± 3.4)	n/a	13.5	22.5	↑ 1
MOLENAARS					
Conductivity	2.72 (± 0.41)	15	2.21	3.36	↓ 1
pH	6.25 (± 0.61)	10	5.40	6.92	↑ 1
Alkalinity	0.090 (± 0.010)	11	0.072	0.096	↓ 31
Na^+	0.147 (± 0.015)	10	0.127	0.167	↓ 1
K^+	0.013 (± 0.001)	11	0.011	0.016	↑ 2
Mg^{2+}	0.029 (± 0.004)	14	0.022	0.034	0
Ca^{2+}	0.022 (± 0.015)	67	0.003	0.037	↑ 45
$C\ell^-$	0.136 (± 0.025)	18	0.092	0.154	↓ 6
$SO4^{2-}$	0.021 (± 0.003)	14	0.016	0.025	↓ 11
PO_4-P	0.852 (± 0.255)	30	0.683	1.356	↓ 27
NO_3-N	10.200 (± 2.315)	23	7.277	12.682	↑ 22
NO_2-N	0.110 (± 0.027)	25	0.070	0.148	↑ 17
SiO_2-Si	22.313 (± 39.313)	176	4.306	102.491	↑ 1
Riffle O_2	98.1 (± 6.9)	7	87.8	105.8	↓ 4
Run O_2	87.3 (± 5.0)	6	78.3	92.2	↓ 11
Pool O_2	66.6 (± 8.7)	13	51.6	76.0	↓ 19
Min Temp	15.2 (± 3.5)	n/a	10.0	20.5	↑ 8
Max Temp	23.7 (± 5.2)	n/a	16.0	28.9	↓ 5
Instant Temp	18.9 (± 4.8)	n/a	12.8	26.0	↑ 22

Table 5.1 Continued. * = estimated minimum NO_3-N levels for the Du Toits and Riviersonderend for trace concentrations below the 0.009 μmol ℓ^{-1} detection limit.

SITE AND CHEMICAL VARIABLE	NATURAL TEMPORAL RANGE (Dec-May) MEAN (± SD)	CV	MIN	MAX	IMPACT VERSUS CONTROL LOCATION % DIFFERENCE IN MEAN VALUES (Feb-Mar)
DU TOITS					
Conductivity	3.23 (± 0.46)	14	2.67	3.88	↓ 4
pH	5.11 (± 0.17)	3	4.90	5.34	↓ 1
Alkalinity	0.048 (± 0.019)	40	0.024	0.078	↓ 30
Na^+	0.170 (± 0.014)	8	0.153	0.194	↑ 2
K^+	0.004 (± 0.001)	23	0.002	0.005	↑ 17
Mg^{2+}	0.039 (± 0.008)	20	0.029	0.048	↑ 4
Ca^{2+}	0.020 (± 0.006)	31	0.013	0.028	↓ 14
$C\ell^-$	0.214 (± 0.031)	14	0.161	0.241	↑ 16
$SO4^{2-}$	0.024 (± 0.005)	21	0.016	0.031	↑ 12
PO_4-P	0.426 (± 0.139)	33	0.302	0.683	↓ 24
NO_3-N	0.716 (± 1.133)	158	*0.005	2.585	↓ 59
NO_2-N	0.086 (± 0.055)	64	0.011	0.180	↓ 7
SiO_2-Si	9.371 (± 17.122)	183	0.320	44.128	↓ 43
Riffle O_2	93.1 (± 11.6)	12	70.6	102.5	↓ 4
Run O_2	82.5 (± 11.6)	14	66.2	98.4	↑ 1
Pool O_2	60.0 (± 19.8)	33	40.0	93.3	↑ 4
Min Temp	15.5 (± 3.0)	n/a	10.5	19.0	↑ 2
Max Temp	23.3 (± 3.0)	n/a	20.0	26.6	↑ 3
Instant Temp	17.9 (± 3.1)	n/a	14.1	23.0	↑ 5
RIVIERSONDEREND					
Conductivity	3.30 (± 0.66)	20	2.55	4.13	↑ 7
pH	4.61 (± 0.35)	8	4.00	5.04	↓ 1
Alkalinity	0.026 (± 0.012)	48	0.006	0.036	↓ 8
Na^+	0.151 (± 0.020)	13	0.130	0.177	↑ 4
K^+	0.004 (± 0.001)	39	0.002	0.006	↑ 37
Mg^{2+}	0.046 (± 0.010)	22	0.036	0.060	↓ 21
Ca^{2+}	0.016 (± 0.010)	59	0.005	0.028	↓ 41
$C\ell^-$	0.204 (± 0.006)	3	0.199	0.214	↑ 8
$SO4^{2-}$	0.023 (± 0.002)	10	0.020	0.025	↑ 38
PO_4-P	0.381 (± 0.039)	10	0.347	0.437	↓ 3
NO_3-N	0.012 (± 0.016)	140	*0.005	0.045	↓ 14
NO_2-N	0.064 (± 0.018)	28	0.050	0.096	↑ 24
SiO_2-Si	9.692 (± 13.412)	138	2.633	36.655	↓ 22
Riffle O_2	97.6 (± 8.3)	9	81.0	103.4	↓ 1
Run O_2	80.7 (± 10.9)	14	66.7	93.4	↓ 4
Pool O_2	59.3 (± 12.9)	22	37.8	70.4	↑ 15
Min Temp	17.3 (± 5.0)	n/a	8.8	23.5	↑ 1
Max Temp	22.8 (± 4.6)	n/a	14.3	27.0	↑ 1
Instant Temp	19.7 (± 4.2)	n/a	13.1	24.2	↑ 6

Table 5.2 Results of Mann-Whitney U tests for comparisons of water chemistry between control (C) and impact (I) locations, for each site and variable. EL – Elands; MO – Molenaars; DU - Du Toits; RI - Riviersonderend. Two-sided exact *P* values are presented, with significant values shaded. Number of samples per location (*n*) indicated in parentheses; for the flowing river channel, six monthly samples were taken per location, but for select variables additional samples were taken from isolated standing waters (EC, pH, and pool O_2) or at more frequent intervals (temperature).

VARIABLE	SITE LOCATION PAIR Control (*n*) vs. Impact (*n*)	U	*P*
Conductivity	ELC (9) vs. ELI (8)	25.5	0.321
	MOC (9) vs. MOI (9)	34.5	0.605
	DUC (9) vs. DUI (9)	35.5	0.666
	RIC (9) vs. RII (9)	25.0	0.190
pH	ELC (9) vs. ELI (8)	29.5	0.541
	MOC (9) vs. MOI (9)	32.0	0.489
	DUC (9) vs. DUI (9)	34.0	0.605
	RIC (9) vs. RII (9)	22.5	0.113
Alkalinity	ELC (6) vs. ELI (6)	12.5	0.394
	MOC (6) vs. MOI (6)	7.0	0.093
	DUC (6) vs. DUI (6)	10.5	0.240
	RIC (6) vs. RII (6)	16.0	0.818
Na^+	ELC (6) vs. ELI (6)	11.0	0.310
	MOC (6) vs. MOI (6)	12.0	0.394
	DUC (6) vs. DUI (6)	9.0	0.180
	RIC (6) vs. RII (6)	13.0	0.485
K^+	ELC (6) vs. ELI (6)	15.0	0.699
	MOC (6) vs. MOI (6)	15.0	0.699
	DUC (6) vs. DUI (6)	14.0	0.589
	RIC (6) vs. RII (6)	17.0	0.937
Mg^{2+}	ELC (6) vs. ELI (6)	12.0	0.394
	MOC (6) vs. MOI (6)	14.0	0.589
	DUC (6) vs. DUI (6)	13.0	0.485
	RIC (6) vs. RII (6)	17.0	0.937
Ca^{2+}	ELC (6) vs. ELI (6)	15.0	0.699
	MOC (6) vs. MOI (6)	13.0	0.485
	DUC (6) vs. DUI (6)	3.0	0.015
	RIC (6) vs. RII (6)	15.0	0.699
$C\ell^-$	ELC (6) vs. ELI (6)	17.0	0.937
	MOC (6) vs. MOI (6)	17.0	0.937
	DUC (6) vs. DUI (6)	17.0	0.937
	RIC (6) vs. RII (6)	17.0	0.937
SO_4^{2-}	ELC (6) vs. ELI (6)	15.0	0.699
	MOC (6) vs. MOI (6)	17.0	0.937
	DUC (6) vs. DUI (6)	16.0	0.818
	RIC (6) vs. RII (6)	13.0	0.485

Table 5.2 Continued.

VARIABLE	SITE LOCATION PAIR Control (*n*) vs. Impact (*n*)	U	*P*
PO_4-P	ELC (6) vs. ELI (6)	13.5	0.485
	MOC (6) vs. MOI (6)	13.0	0.485
	DUC (6) vs. DUI (6)	18.0	1.063
	RIC (6) vs. RII (6)	16.0	0.818
NO_3-N	ELC (6) vs. ELI (6)	14.0	0.589
	MOC (6) vs. MOI (6)	18.0	1.063
	DUC (6) vs. DUI (6)	18.0	1.063
	RIC (6) vs. RII (6)	17.5	0.937
NO_2-N	ELC (6) vs. ELI (6)	11.0	0.310
	MOC (6) vs. MOI (6)	14.0	0.589
	DUC (6) vs. DUI (6)	17.0	0.937
	RIC (6) vs. RII (6)	4.5	0.026
SiO_2-Si	ELC (6) vs. ELI (6)	15.0	0.699
	MOC (6) vs. MOI (6)	18.0	1.063
	DUC (6) vs. DUI (6)	17.0	0.937
	RIC (6) vs. RII (6)	12.5	0.394
Riffle O_2	ELC (6) vs. ELI (6)	11.5	0.310
	MOC (6) vs. MOI (6)	16.0	0.818
	DUC (6) vs. DUI (6)	17.5	0.937
	RIC (6) vs. RII (6)	16.5	0.818
Run O_2	ELC (6) vs. ELI (6)	1.0	0.004
	MOC (6) vs. MOI (6)	11.0	0.310
	DUC (6) vs. DUI (6)	17.0	0.937
	RIC (6) vs. RII (6)	12.0	0.394
Pool O_2	ELC (8) vs. ELI (7)	10.0	0.040
	MOC (8) vs. MOI (9)	27.0	0.423
	DUC (8) vs. DUI (9)	36.0	1.037
	RIC (8) vs. RII (9)	33.0	0.815
Min Temp	ELC (15) vs. ELI (15)	99.0	0.595
	MOC (12) vs. MOI (14)	68.5	0.432
	DUC (13) vs. DUI (13)	75.0	0.650
	RIC (15) vs. RII (17)	89.5	0.153
Max Temp	ELC (15) vs. ELI (15)	112.5	1.000
	MOC (12) vs. MOI (14)	81.5	0.899
	DUC (13) vs. DUI (13)	64.5	0.311
	RIC (14) vs. RII (17)	116.0	0.922
Instant Temp	ELC (17) vs. ELI (16)	119.0	0.557
	MOC (12) vs. MOI (16)	82.0	0.537
	DUC (14) vs. DUI (14)	76.0	0.329
	RIC (13) vs. RII (13)	80.0	0.840

Based on time series plots (Appendix 5.1e) and one-way ANOVA and Tukey HSD results (Table 5.3), it was evident that the Riviersonderend and Du Toits sites grouped at naturally far higher concentrations of the dominant anion, $C\ell^-$ (0.161 mmol ℓ^{-1}, Feb, to 0.241 mmol ℓ^{-1}, Mar), than the Elands and Molenaars sites (0.065 mmol ℓ^{-1}, Apr, to 0.154 mmol ℓ^{-1}, Jan) ($F_{3,\ 44} = 78.198$, $P << 0.001$). This was an opposite trend to that of K^+ (Appendix 5.1b). Chloride was naturally stable at low flows, exhibiting lowest variability in the Riviersonderend reach (CV = 3%). Despite experimental discharge reduction in the Molenaars reach, there did not appear to be a pronounced effect on [$C\ell^-$] (Table 5.1 and Appendix 5.1e). A 16% increase in [$C\ell^-$]

above the natural, peak dry-season average was recorded for the Du Toits location (Table 5.1), but the general pattern of site concentrations suggested that the markedly lower natural value for February is most likely anomalous and the cause of the apparent flow-reduction effect. Chloride levels were highly similar in both Riviersonderend locations during December-January, but concentrations were consistently higher in the impact location throughout the subsequent impact and post-impact phases (Appendix 5.1e) until early May, when natural increases in discharge were recorded (Figure 4.7). The result suggested some effect of large-scale flow reduction which was difficult to substantiate further, despite the otherwise inherently low variability in [$C\ell^-$]. This was due to the lack of a marked increase in February-March mean value relative to control data (only 8% - Table 5.1), as well as the existence of changes of similar magnitude over time at the control site (but see Q-C trends).

Although the Elands site showed significantly lower and the Riviersonderend generally higher SO_4^{2-} concentrations than the remaining sites ($F_{3, 44} = 3.729$, $P = 0.018$), further separation of sites was not possible (Tukey HSD results, Table 5.3). Natural mean concentrations were similar across sites ($\bar{x}$ = 0.019-0.024 mmol ℓ^{-1}) with fairly low variability, except for the control site (CV_{max} of 30%) (Table 5.1 and Appendix 5.1f). The elevated early February value of 0.040 mmol ℓ^{-1} for the Riviersonderend impact location (as compared with a natural background value of 0.023 mmol ℓ^{-1}; Appendix 5.1g), and associated 38% difference in means during the flow-reduction phase provided evidence of a possible effect of abnormally low discharges, further supported by Q-C relationships.

River pH and total alkalinity

Time series of pH and total alkalinity (TA) are illustrated in Figure 5.2 and Appendix 5.1g, respectively. The two variables were significantly positively correlated ($r = 0.66$, $P < 0.05$). Dallas and Day (1993) observed that the low carbonate and bicarbonate waters of rivers of the Western Cape, which include the study sites, are more likely to show marked pH fluctuations than more buffered waters. No significant differences between locations at each site were found for pH or total alkalinity, on the basis of Mann-Whitney U tests (Table 5.2). Results of one-way ANOVAs indicated though that the waters of the Riviersonderend River were naturally highly acidic relative to those of the other sites ($\bar{x}$ = 4.6 ± 0.4; Table 5.1) ($F_{3, 44} = 33.477$, $P << 0.001$; Table 5.3) and hence, of lowest buffering capacity. Clear separation of the remaining sites was evident (Tukey HSD results, Table 5.3), with the Du Toits and Elands grouping at mean pH values of 5.1 and 5.6, respectively (Table 5.1). The natural range in mainstream pH for the former site (based on control data) was only 0.4 pH units, compared with 0.8 pH units for the latter site (Table 5.1). The Molenaars reach showed the most elevated, natural average pH, 6.3 (with a total range of 1.5 pH units). Overall, pH was a highly conservative variable, as anticipated, with CVs at or below 10% (Table 5.1).

During the months of naturally lowest flow, and with unnatural discharge reductions, responses in pH were inconsistent (Table 5.1; see also Q-C trends). For the Molenaars site, pH values were generally similar in

both locations, and among months, regardless of flow reduction (Figure 5.2). Moreover, although the range in pH was wide for the highly flow-impacted locations of the Du Toits and Riviersonderend sites, it was similar for the control site (Table 5.1). For the Riviersonderend, for instance, the natural range in mainstream pH was 1.0 pH units, as compared with 1.7 pH units for the impact location. However, the time series of pH at this site indicated divergence between control and impacted locations during the impact and post-impact phases, following highly similar pre-impact figures (Figure 5.2). Initially higher in pH than under natural conditions, within the impacted location the river subsequently became more acidic throughout February-April, tending towards naturally low levels again only in May, with the action of higher flows (Figure 4.7).

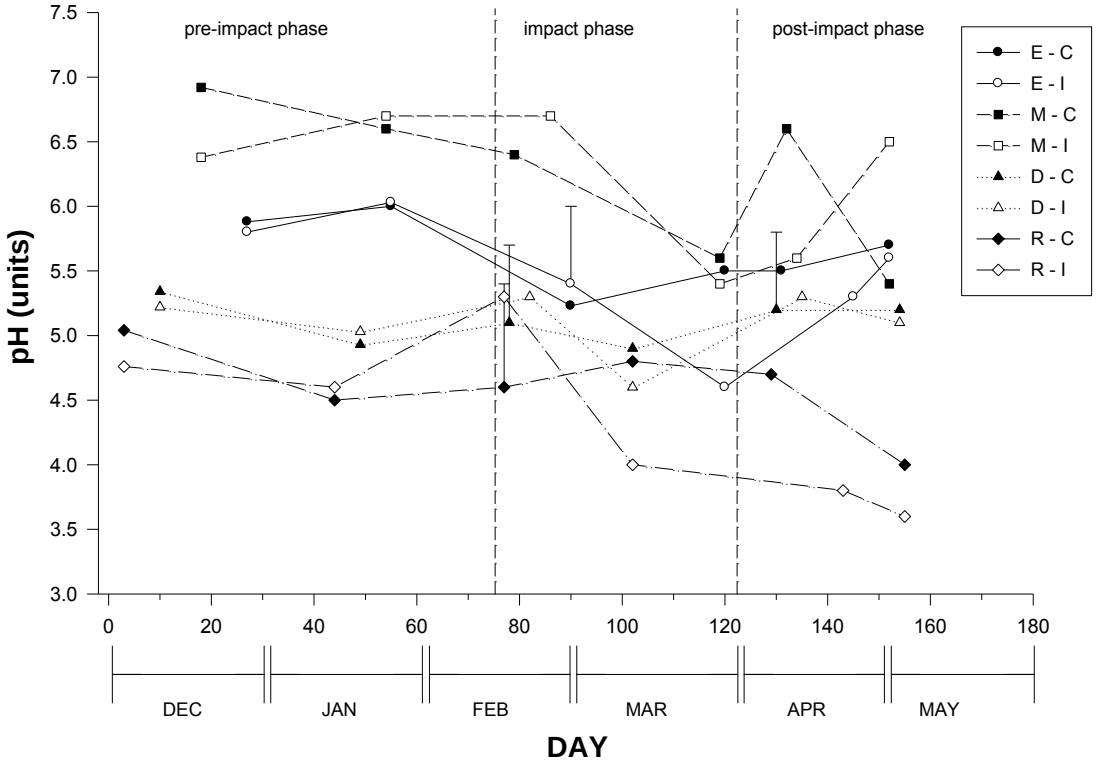


Figure 5.2 **Changes in pH at the sites during the phases of the low flow study**. Demarcation of the impact phase is approximate. Upper error bars indicate pH values in standing pools, where pH was ≥ 10% of mainstream pH. E = Elands; M = Molenaars; D = Du Toits; R = Riviersonderend; C = control; I = impact.

Assessment of the potential influence on pH of loss of habitat connectivity, revealed that in isolated standing pools in locations experiencing natural low flows, pH values were generally slightly higher than those of the mainstream, and only occasionally lower or the same (Figure 5.2; see also Figure 5.6 below, as an example). In isolated pools within flow-impacted locations there was no obvious pattern, with no marked differences in pH between the mainstream and isolated pools (Figures 5.2 and 5.6). Considering differences in pH in pools

that exceeded 10% of mainstream values, only pH increases were observed, and solely for control locations (Figure 5.2). Moreover, such differences were not greater than a single pH unit and typically occurred in the month of lowest flow; diel changes of 1 pH unit can occur naturally (Dallas *et al.* 1998).

Table 5.3 **Results of one-way ANOVAs for comparisons of water chemistry among the sites**. H_0: Elands (EL) = Molenaars (MO) = Du Toits (DU) = Riviersonderend (RI), for each chemical variable sampled, α = 0.05. Data for control and impact locations were pooled (*n* = 48), thereby including data potentially reflecting effects of extreme flow reduction. For variables showing significant differences among sites (*P* with asterisk), site groupings resulting from *post hoc* Tukey HSD tests are indicated, with the sequence of sites from lowest to highest mean value for each variable. In several instances, Tukey results were inconclusive and site(s) straddled two groups. NS = no significant difference among sites. XXXX denotes group membership.

VARIABLE	*F* (*df* Effect = 3, *df* Error = 44)	*P*	TUKEY HSD RESULTS			
			Site	Group 1	Group 2	Group 3
Conductivity	15.230	0.000*	EL	XXXX		
			MO		XXXX	
			DU		XXXX	XXXX
			RI			XXXX
pH	33.477	0.000*	RI	XXXX		
			DU		XXXX	
			EL		XXXX	
			MO			XXXX
Alkalinity	25.326	0.000*	RI	XXXX		
			DU	XXXX		
			EL		XXXX	
			MO		XXXX	
Na^+	10.747	0.000*	EL	XXXX		
			MO	XXXX	XXXX	
			RI		XXXX	
			DU			XXXX
K^+	74.046	0.000*	RI	XXXX		
			DU	XXXX		
			EL		XXXX	
			MO			XXXX
Mg^{2+}	12.719	0.000*	MO	XXXX		
			EL	XXXX		
			DU		XXXX	
			RI		XXXX	
Ca^{2+}	2.252	0.096	NS			
$C\ell^-$	78.198	0.000*	EL	XXXX		
			MO	XXXX		
			RI		XXXX	
			DU		XXXX	
SO_4^{2-}	3.729	0.018*	EL	XXXX		
			MO	XXXX	XXXX	
			DU	XXXX	XXXX	
			RI		XXXX	
PO_4-P	56.705	0.000*	RI	XXXX		
			DU	XXXX		
			MO		XXXX	
			EL			XXXX

Table 5.3 Continued.

VARIABLE	*F* (*df* Effect = 3, *df* Error = 44)	*P*	TUKEY HSD RESULTS			
			Site	Group 1	Group 2	Group 3
Log_{10} NO_3-N	343.178	0.000*	RI DU MO EL	XXXX XXXX	XXXX	XXXX
NO_2-N	1.669	0.187	NS			
Log_{10} SiO_2-Si	0.727	0.542	NS			
Riffle O_2	1.453	0.240	NS			
Run O_2	0.990	0.406	NS			
Pool O_2	0.061	0.980	NS			
Min Temp	0.636	0.596	NS			
Max Temp	0.246	0.864	NS			
Instant Temp	0.518	0.672	NS			

One-way ANOVA and Tukey HSD results yielded only two highly significant groups of sites for total alkalinity ($F_{3, 44}$ = 25.326, $P << 0.001$; Table 5.3), with the low-pH Riviersonderend and Du Toits sites having correspondingly lower alkalinities than the other site pair (Table 5.1 and Appendix 5.1g). Over all sites, natural mean alkalinities ranged from 0.026 to 0.090 mEq ℓ^{-1} (Table 5.1). Lowest alkalinities were recorded for the Riviersonderend site, in May (*c.* 0.005 mEq ℓ^{-1}). In contrast with pH, TA was shown to be naturally variable throughout the study period, at all sites bar the Molenaars (CVs of 40-48% versus 11%; Table 5.1). This variability, particularly in the control site (40%), rendered any differences in alkalinity observed at flow-impacted sites difficult to assess in terms of their actual relevance. Thus, although flow reduction to levels below natural absolute minima for the three experimental sites (Figures 4.9b-d) resulted in consistent reductions in TA of 8-31% during the period of flow reduction (Table 5.1), their ecological significance is unlikely when viewed in conjunction with Q-C relations and control site trends.

Nutrients and silicon

Spatiotemporal variations in NO_3-N, NO_2-N and PO_4-P are illustrated in Appendix 5.1h-j. Ammonium was excluded, with concentrations below the 0.2 mg ℓ^{-1} detection limit in all instances (but see Table 5.6 for historical figures). The most significant, natural inter-site differences in water chemistry overall were found for nitrate concentrations ($F_{3, 44}$ = 343.178, $P << 0.001$), resulting in three distinct site groups (Table 5.3). Nitrates were low at the Riviersonderend, particularly, and Du Toits sites, demonstrating their naturally oligotrophic character ($\bar{x}$ = 0.012 ± 0.016 µmol ℓ^{-1}, Riviersonderend, and $\bar{x}$ = 0.716 ± 1.133 µmol ℓ^{-1}, Du Toits; Table 5.1). Generally, only trace concentrations were recorded (< 0.009 µmol ℓ^{-1}), and $[NO_3\text{-}N]_{max}$ was only 2.585 µmol ℓ^{-1}, for the Du Toits site in May. Variability in this chemical constituent was high, with CVs of 140% for the Riviersonderend and 158% for the Du Toits (Table 5.1). In contrast, the more

anthropogenically disturbed Molenaars and Elands reaches (Chapter 2) exhibited mild nutrient enrichment, with peak NO_3-N levels of 12.682 μmol ℓ^{-1}, and 18.001 μmol ℓ^{-1}, respectively (Table 5.1 and Appendix 5.1h). Moreover, variability over time was considerably lower, at 21% and 23% (Table 5.1). For all sites, nitrate maxima were not necessarily associated with the month of lowest flow. Furthermore, responses to unnaturally low flows were inconsistent and masked by the elevated natural variability for two of the three experimental sites. Although there was a mean increase in [NO_3-N] of 22% relative to control conditions for the Molenaars, decreases in nitrates of 14% (Riviersonderend) and 59% (Du Toits) occurred with greatest reduction in discharge (Table 5.1).

Significant differences in nutrient concentrations between locations at sites were found only for nitrite, in the Riviersonderend River (U = 4.5, P = 0.026; Table 5.2). Examination of the corresponding time series (Appendix 5.1i) indicated that the difference was probably attributable to natural variation early in the dry season. There were no marked inter-site differences in nitrite concentrations, with a low range in means of 0.064-0.110 μmol ℓ^{-1} (Tables 5.3 and 5.1, respectively). However, NO_2-N concentrations were moderately variable over time (CV_{max} of 64% for the Du Toits River; Table 5.1). There was no discernible, consistent effect of unnaturally low flows on nitrites (Table 5.1 and Appendix 5.1i; see also Q-C relationship).

Analysis of PO_4-P dynamics across sites and months (Appendix 5.1j) revealed significantly higher natural concentrations in the Elands ($\bar{x}$ = 1.604 ± 0.408 μmol ℓ^{-1}), followed by the Molenaars ($\bar{x}$ = 0.852 ± 0.255 μmol ℓ^{-1}), and with a separate group comprising the other sites at low means of 0.426 and 0.381 μmol ℓ^{-1}, respectively ($F_{3, 44}$ = 56.705, P << 0.001, and Tukey HSD results; Table 5.3). At artificially extreme low flows, consistent declines in PO_4-P were found, from a marginal 3% decrease for the Riviersonderend to decreases of 24% and 27% for the Du Toits and Molenaars impact locations, respectively (Table 5.1). The degree to which the recorded changes might be significant was impossible to assess, as a result of the observed 23% decrease in [PO_4-P] at the control site during the same months, as well as conflicting Q-C results.

Although there were no major increases or decreases in No_x-N (inorganic-N as nitrate and nitrite combined) or [PO_4-P] at extreme low flows, changes in algal densities and composition, and instream macrophyte decomposition (Section 5.2.3) were indicative of at least localised interrelationships between flow and nutrient release and uptake by vegetation.

Spatial and temporal changes in SiO_2-Si are depicted in Appendix 5.1k. Silicon concentrations did not differ significantly between locations at any of the sites (Table 5.2) or among sites (Table 5.3) at low flows, with an overall range of 0.320-113.879 μmol ℓ^{-1}. Notably, SiO_2-Si was the most inherently variable chemical constituent sampled (CVs ranging from 123%, Elands, to 183%, Du Toits), under natural flow conditions (Table 5.1; see also Chapter 2). Silicon concentrations were similarly low in December and January at all

sites, increasing to peak levels midsummer for the Elands, and in April-May for the other sites. Natural variability rendered any patterns in [SiO_2-Si] with unnatural flow reduction impossible to discern. For instance, during the impact phase, a difference in [SiO_2-Si] of 63% between locations was found under control conditions, rendering inconclusive the 43% and 22% decreases recorded for the Du Toits and Riviersonderend impact locations, respectively (Table 5.1). Furthermore, although a dramatic increase in concentration in April, for the impacted location of the Du Toits River, followed extreme flow reduction, similar sharp increases in concentration were evident in the control site.

Dissolved oxygen and biotope differences in oxygen levels

Patterns in dissolved oxygen (DO, as % saturation), observed at each site, for the main biotopes from which benthic macroinvertebrates were sampled (Section 3.5.1), are illustrated in Figure 5.3; trends in DO as mg ℓ^{-1} were much the same. As naturally, DO fluctuates diurnally (Dallas *et al.* 1994), the figures reflected only broad spatiotemporal variation.

Although there were no within-reach differences in riffle DO at any of the sites at low flows, Mann-Whitney U tests detected significant differences in DO in runs (U = 1.0, $P = 0.004$) and pools (U = 10.0, $P = 0.040$) in the Elands River (Table 5.2). Examination of monthly [O_2] for runs, indicated that the divergence between locations was mostly a function of elevated control values during early summer and autumn (Figure 5.3). Intra-site differences in pool O_2 were due to lower levels in the impact location until at least April (Figure 5.3). There was also a tendency for runs and pools to exhibit higher overall variability than riffles across all the sites (pool CVs = 13-33% and run CVs 6-14%, versus CVs = 4-12%, for riffles; Table 5.1). Analysis of variance yielded no significant differences in O_2 per biotope among sites, with highly similar means and ranges for each site over the study period (Figure 5.3; Tables 5.3 and 5.1, respectively). Significantly, however, there were consistent, distinct differences in oxygen levels among biotopes (one-way ANOVA, $F_{2, 159} = 174.95$, $P << 0.001$). As expected, riffles had highest O_2 levels, near saturation ($\bar{x} = 96.6 \pm 7.3\%$), followed by runs ($\bar{x} = 85.2 \pm 8.8\%$) (Tukey HSD test for unequal N). Pool oxygen levels were far lower and most variable ($\bar{x} = 58.7 \pm 14.6\%$) (Table 5.1).

There was no conclusive reduction in O_2 levels due to extremely low flows, even in isolated pools (Figure 5.3; see also Q-C results), though the lowest DO level of 35% was recorded in a pool in the flowing but impacted section of the Molenaars reach, during the month of lowest flow. For the other two experimental sites, the Du Toits and Riviersonderend, lowest O_2 levels were recorded under conditions of natural low flow in pools, at 40% and 38%, respectively (Table 5.1). Similarly, at the control site, the lowest [O_2] (39%) was recorded in a pool in February.

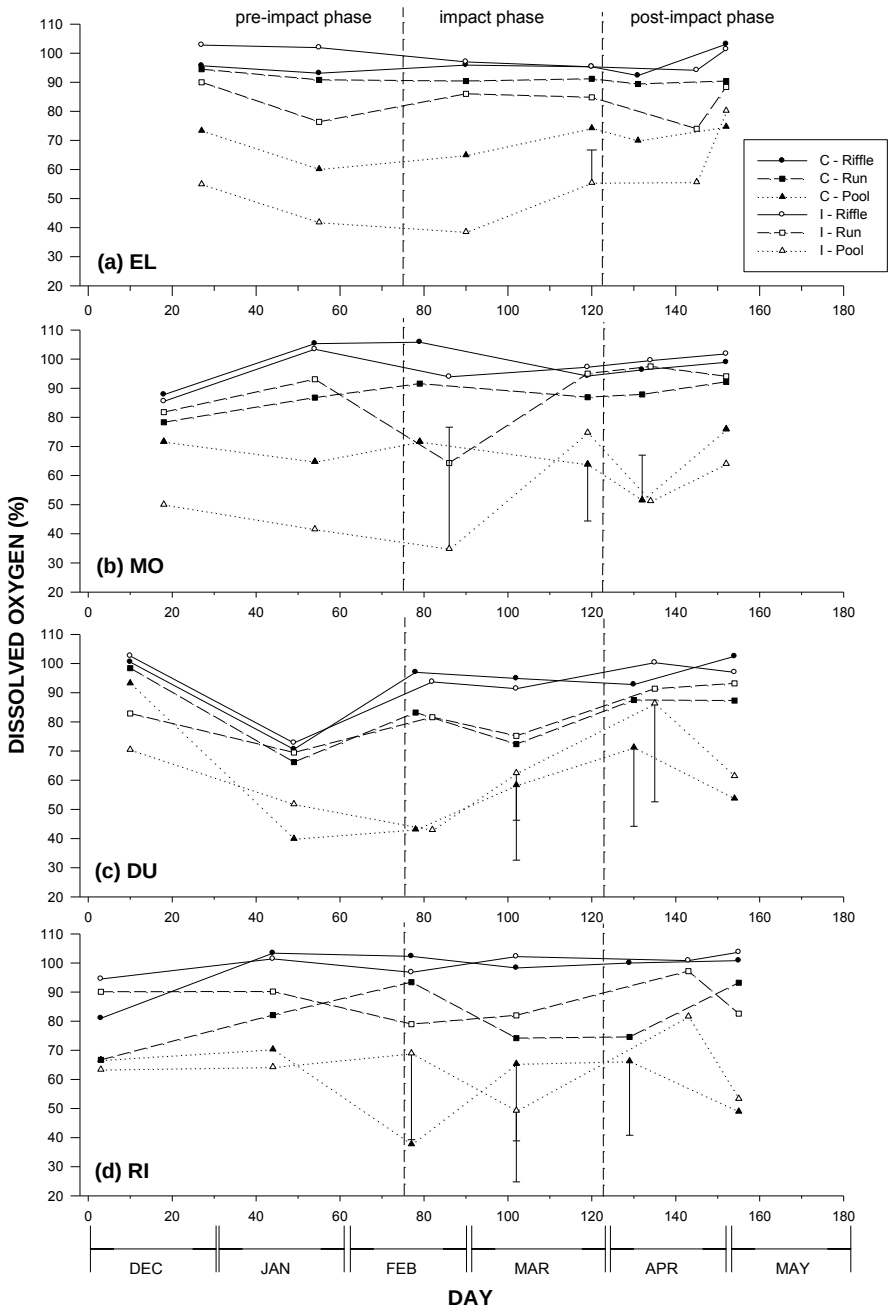


Figure 5.3 Changes in dissolved oxygen (% saturation) for dominant biotopes at the sites during the phases of the low flow study. (a) EL = Elands; (b) MO = Molenaars; (c) DU = Du Toits; and (d) RI = Riviersonderend. Demarcation of the impact phase is approximate. Error bars indicate oxygen concentrations in isolated standing pools that were ≥ 10% of O_2 levels in mainstream pools.

Water temperature ranges and differences across biotopes

All locations (Table 5.2) and sites (Table 5.3) exhibited broadly similar temperature conditions (maxima, minima and instantaneous temperatures) (Appendix 5.1l). Natural maxima of about 27-29 °C and minima in the order of 9-10 °C were recorded, with both measures exhibiting similar degrees of variability (Table 5.1). Elevated temperatures (and absolute maxima) tended to coincide with the onset of low flows in early

summer. Temperatures then remained fairly constant over the dry season, before declining again from April onwards. Overall minima were coincident with the changes in season from summer to autumn, including decreases in ambient air temperature and photoperiod, as well as in the magnitude (Figure 4.7) of higher flows. Natural, absolute differences in temperature at sites, over December to May, were lowest at 16.7 °C for the Du Toits site, followed by Elands (18.6 °C), Riviersonderend (18.7 °C), and highest (18.9 °C) for the Molenaars reach. Foothill reaches tended to exhibit slightly higher maxima and minima than the cooler mountain-stream and transitional zones (Table 2.3), although the difference was not marked midsummer. Under natural conditions, intra-reach variability in temperature was low for all sites except the Riviersonderend, which showed modest variation in minima particularly (Appendix 5.1l).

With extreme flow reduction, no effects on temperature were manifested (see also Q-C results). Comparisons of percentage differences in average instantaneous temperature for the lowest flow period of the study showed that values for the impact locations at experimental sites were consistently elevated above natural values, although only markedly so in the Molenaars reach (22%, relative to 1% for the control site; Table 5.1). In contrast, only slight differences between locations at unnatural low flows were apparent for maximum and minimum temperatures (Table 5.1). Moreover, the recorded range in temperature during the impact phase of the study did not follow any trend in relation to the magnitude of flow reduction. For the control site, the temperature difference was about 11.9 °C over February-March. For the sites at which flows were manipulated, the temperature difference was lowest for the Du Toits site, at 9.5 °C, greater for the Molenaars site (10.1 °C), and highest for the Riviersonderend reach, at 11.7 °C. For only the first two sites were differences marginally lower than under natural low flows.

Comparison of instantaneous temperatures among the main biotopes sampled at the sites, measured at the same time as DO, indicated virtually identical values ($\bar{x}$ = 18.7-18.8 ± 3.8-4.0 °C), irrespective of biotope type (one-way ANOVA, $F_{2, 159} = 0.009$, $P = 0.991$).

5.2.2 Concentration-discharge trends for chemical variables, with emphasis on flow reduction

Insights into general trends in water chemistry variables in relation to flow reduction were gained through the establishment of discharge-concentration relationships. Attempts were made to identify any key chemical variables from a low flow perspective, and to categorize them in terms of low flow response. In terms of the chapter objectives, it was assumed that if a distinct relationship existed between a chemical constituent and discharge, it provided evidence that the constituent might potentially exert a secondary influence on invertebrates at low flows.

Best-fit relationships between individual water chemistry variables and normalised daily discharge are summarised in Table 5.4, for the particular site subgroup affinities previously identified on the basis of ANOVA and *post hoc* Tukey HSD results (Table 5.3) (Section 3.3.2). In the majority of instances,

relationships between low flows and chemical constituents were weak to non-existent (Table 5.4). Moderate relationships ($0.2 < R^2 < 0.5$) were apparent in only five instances, and just for select subsets of sites. Moreover, few variables showed consistent trends among sites, this despite *a priori* evidence of highly similar chemistry among sites (Chapter 2). Over the narrow range of discharges examined, R^2 values for non-linear trends often were similar to those for linear relationships, but a tendency for non-linearity at the low-flow end of several Q-C curves was noteworthy.

Consistent increases in conductivity with flow reduction were found for all site groups, including the strongest relationship across all chemical variables, for the Molenaars site ($R^2 = 0.50$) (Figure 5.4). Increases in conductivity were generally apparent with extreme flow reduction in the Du Toits and Riviersonderend reaches, especially with biotope isolation and the development of standing waters (Table 5.4 and Appendix 5.2a). For all experimental sites, however, there were also instances where isolated pools at natural discharges yielded similar conductivities to flow-impacted pools (Appendix 5.2a). Data collected from the control site clearly showed that both flowing-water and isolated, standing-water patches had similar conductivities under natural flows (Appendix 5.2b).

Trends in major ions with flow reduction tended to be weak or non-apparent, as well as inconsistent in direction among sites/site groups (Table 5.4). However, Na^+ showed a similarly consistent, positive relationship at low flows to that of conductivity. Potassium concentrations increased with flow reduction at all experimental sites, compared with a decrease under natural flow conditions (Elands), but the relationship remained weak. Similarly, [$C\ell^-$] increased with decreasing discharge at the two sites for which the greatest proportion of dry season flow was diverted, while a negative relationship was obtained for the Molenaars (36% flow reduction) and Elands (control) sites. For [SO_4^{2-}], the Q-C trend with flow reduction was negative at the control site ($r^2 = 0.31$; Table 5.4 and Appendix 5.2c), while the most distinctly positive relationship ($r^2 = 0.35$), obtained for the Riviersonderend site, was due to elevated SO_4^{2-} levels at discharges below natural minima (Table 5.4 and Appendix 5.2d).

Relationships between discharge and pH were slight, and not consistent among site groups (Table 5.4), supporting the results from time series analysis (Section 5.2.1). The lack of influence of manipulated flow disturbance on pH, as well as the tendency for isolated control pools to exhibit pH values greater than those of corresponding flowing-water patches, is illustrated in Appendix 5.2e, for the Riviersonderend. Similarly inconclusive results were obtained for alkalinity in the mainstream (Table 5.4).

Table 5.4 Relationships between daily discharge (Q_{inst}: Q_{50}; $m^3 s^{-1}$) and water chemistry variables. Site data were pooled in accordance with one-way ANOVA results, as were control and impact location data, on the basis of typically non-significant differences among locations over the study period (see text for explanation). Q-C trend with discharge reduction: ↑ = increase or ↓ = decrease in a variable. R^2 = coefficient of determination of the relationship best expressed as a linear, logarithmic (natural), power or exponential function. Moderately strong relationships are differentiated from weak, or slight to non-apparent (s-na), ones by shading. Elands (EL) = Molenaars (MO) = Du Toits (DU) = Riviersonderend (RI).

CHEMICAL VARIABLE AND SITE GROUP(S)	TREND WITH DECREASING Q	EQUATION	R^2
Conductivity (mS m^{-1})			
EL	s-na (↑)	$y = 2.067x^{-0.056}$	0.042
MO + DU	↑	$y = 2.780x^{-0.110}$	0.160
MO	↑	$y = 3.641e^{-0.459x}$	0.496
DU + RI	↑	$y = 3.734e^{-0.169x}$	0.125
RI	↑	$y = 3.957e^{-0.189x}$	0.130
pH			
RI	s-na (↑)	y = -0.122Ln(x) + 4.431	0.040
DU + EL	s-na (↑)	y = -0.142x + 5.422	0.011
MO	↓	$y = 5.646e^{0.149x}$	0.104
Total Alkalinity $HCO3^-$ (mEq ℓ^{-1})			
RI + DU	s-na (↑)	$y = 0.027x^{-0.166}$	0.035
EL + MO	s-na (↓)	$y = 0.070e^{0.018x}$	0.0001
Na^+ (mmol ℓ^{-1})			
EL + MO	s-na (↑)	$y = 0.146e^{-0.075x}$	0.008
EL	s-na (↑)	$y = 0.146e^{-0.194x}$	0.040
MO + RI	s-na (↑)	$y = 0.156e^{-0.036x}$	0.016
RI	↑	$y = 0.163e^{-0.065x}$	0.065
DU	↑	y = -0.007Ln(x) + 0.173	0.106
K^+ (mmol ℓ^{-1})			
RI + DU	↑	$y = 0.005e^{-0.302x}$	0.170
EL	s-na (↓)	y = 0.002Ln(x) + 0.010	0.034
MO	↑	$y = 0.015e^{-0.142x}$	0.064
Mg^{2+} (mmol ℓ^{-1})			
MO + EL	s-na (↑)	$y = 0.033e^{-0.136x}$	0.027
DU + RI	s-na (↓)	y = 0.002Ln(x) + 0.044	0.038
Ca^{2+} (mmol ℓ^{-1})			
ALL SITES	s-na (↓)	y = 0.001Ln(x) + 0.019	0.005
Cℓ^- (mmol ℓ^{-1})			
EL + MO	↓	y = 0.059x + 0.088	0.231
RI + DU	↑	y = -0.006Ln(x) + 0.210	0.069
SO_4^{2-} (mmol ℓ^{-1})			
EL + MO + DU	↓	$y = 0.018e^{0.223x}$	0.072
EL	↓	$y = 0.011e^{0.808x}$	0.305
MO + DU + RI	↑	y = -0.002Ln(x) + 0.023	0.056
RI	↑	y = -0.004Ln(x) + 0.023	0.349

Table 5.4 Continued.

CHEMICAL VARIABLE AND SITE GROUP(S)	TREND WITH DECREASING Q	EQUATION	R^2
PO_4-P (µmol ℓ^{-1})			
RI + DU	s-na (↓)	y = 0.016Ln(x) + 0.432	0.006
MO	s-na (↓)	$y = 0.814x^{0.151}$	0.043
EL	↑	y = -0.706Ln(x) + 1.237	0.401
Log_{10} NO_3-N (µmol ℓ^{-1})			
RI + DU	↑	$y = 0.035e^{-1.890x}$	0.163
MO	↑	y = -0.083Ln(x) + 1.008	0.135
EL	s-na (↑)	y = -0.067Ln(x) + 1.151	0.047
NO_2-N (µmol ℓ^{-1})			
ALL SITES	s-na (↑)	$y = 0.113e^{-0.330x}$	0.034
Log_{10} SiO_2-Si (µmol ℓ^{-1})			
ALL SITES	s-na (↑)	$y = 0.938e^{-0.259x}$	0.022
Riffle O_2 (%)			
ALL SITES	s-na (↑)	$y = 95.964x^{-0.009}$	0.004
Run O_2 (%)			
ALL SITES	s-na (↑)	$y = 85.877e^{-0.018x}$	0.003
Pool O_2 (%)			
ALL SITES	s-na (↓)	y = 1.400x + 60.105	0.001
Min Temp (°C)			
ALL SITES	s-na (↓)	y = 3.168x + 13.366	0.090
Max Temp (°C)			
ALL SITES	s-na (↓)	y = 3.752x + 19.913	0.082
Instant Temp (°C)			
ALL SITES	s-na (↓)	y = 3.003x + 16.602	0.060

Slight, yet consistent increases in inorganic-N with flow reduction were found, notably for nitrates (Table 5.4). In contrast, for all experimental sites, Q-C relationships for [PO_4-P] were weakly positive, suggesting no distinct decrease in concentration with flow reduction (Table 5.4). The complexity of nutrient interactions doubtless influenced Q-C trends. For the most phosphate-enriched site, the Elands (Table 5.1), a moderate, negative Q-C relationship ($r^2 = 0.40$; Table 5.5) suggested retention of phosphates during the dry season at natural low flows. High variability in [SiO_2-Si] at all sites resulted in no trend in concentration with decreasing discharge (Table 5.4).

No relationship between DO and discharge magnitude over the short-term was found within the flowing section of the channel sampled at each site, for riffles and runs (Table 5.4), which is not surprising given the near saturation levels recorded for these two biotopes. Pool oxygen levels also bore no distinct relationship with discharge magnitude even with biotope isolation at very low flows (Appendix 5.2f). This was most probably as a result of natural fluctuations in DO (Table 5.1).

As suggested by time series analysis (Section 5.2.1), no clear relationships between maximum, minimum, or instantaneous temperature and discharge over the short-term were found within the flowing section of the channel, at any of the sites (Table 5.4).

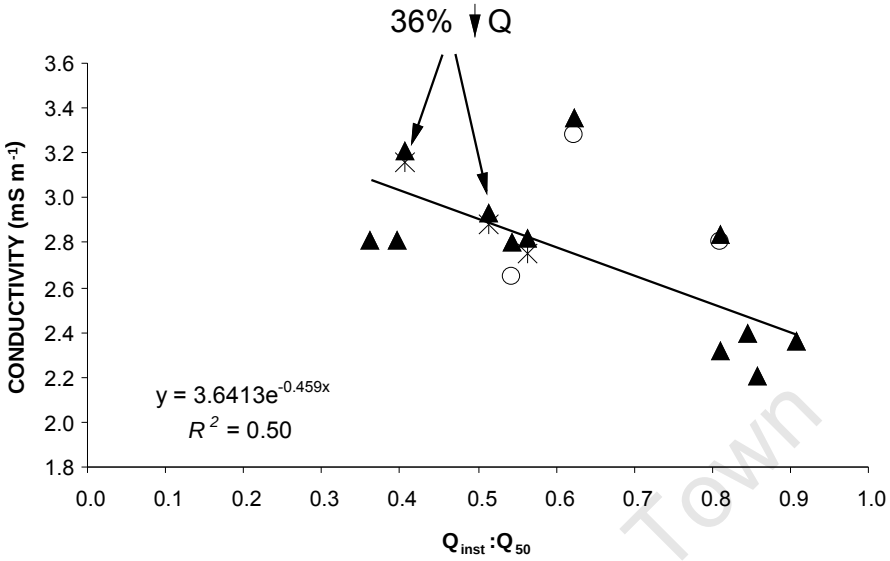


Figure 5.4 **Relationship between conductivity and low flows for the Molenaars site.** Solid triangles represent mainstream samples for which the trend line was fitted, with values representing a 36% discharge reduction indicated. Open circles and stars indicate values for isolated pools under natural and unnatural low flows, respectively.

5.2.3 Potential links between water chemistry and vegetation dynamics at low flows

Shifts in algal assemblages in response to low flows

Algae were sporadically encountered at all sites at the onset of summer low flows, from early December to January (Table 5.5; taxon identifications by P. Joska, Botany Department, U.C.T.). Although species of genera encountered, such as *Mougeotia* and *Ulothrix*, tend to inhabit clean, cooler waters, *Pseudanabaena*, *Oscillatoria* and *Spirogyra* species have been implicated as indicators of nutrient enrichment (P. Joska pers. comm.). Under natural flow regimes, filamentous and other green algae persisted at all sites during February and March, though growth was at similar levels to those of the early dry season.

In contrast, growth in algae above natural levels, as well as exposure and total desiccation in some instances (pers. obs.), were observed in the sections impacted by artificial flow reduction. The smallest increase in algal biomass of all flow-impacted locations occurred within the Du Toits reach, but reflected a marked increase from natural periphyton densities. The *Oscillatoria*-naviculid dominated algal masses found in wide areas of the Molenaars impact location were not encountered under conditions of natural low flow. Heterotrophic slimes indicative of mild nutrient enrichment had previously been reported in slow-flowing areas of the same reach at low flows (Ractliffe and Brown 1994), reflecting a response by riverine bacterial

and fungal communities to increased availability of dissolved organic carbon (Gray 1985). Algal growth at abnormally reduced discharges was especially prolific in the impacted Riviersonderend reach. Although at extreme low flows algal mats were found in all biotopes (except for the few remaining small, fast-flow patches), they were predominant in pools and runs.

For the Du Toits and particularly the Riviersonderend reaches, most desiccated and living algae, as well as much of the observed accumulated organic detritus, were flushed from the flow-impacted sections in April, with reinstatement of the natural flow regime (Figures 4.7c and 4.7d). Within the affected Molenaars reach, however, remnant patches of green filamentous algae and sewage fungus were found in shallow runs for the remainder of the study, possibly due to the more gradual increase in discharge from April onwards (Figure 4.7b), coupled with differences in algal growth habit (Biggs and Close 1989).

Table 5.5 Descriptions of algal assemblages under different low flow conditions at sites.

SITE	EARLY SUMMER NATURAL LOW FLOWS	MID-SUMMER NATURAL LOW FLOWS	MID-SUMMER EXTREME LOW FLOWS
Elands	• Sparsely distributed, minute quantities of filamentous algae, predominantly *Spirogyra* spp.	• Similar assemblage composition and densities as in Dec-Jan.	-
Molenaars	• Small patches comprising *Spirogyra sp.* (20-85% of sample biomass), *Mougeotia* sp. (12-80%), *Ulothrix* sp. (30%), an assortment of unicellular algae (2%) and blue-green alga, *Oscillatoria* (3%). • Blue-green *Pseudanabaena* sp. overlying sand in shallow, marginal slackwaters.	• Similar assemblage composition and densities as in Dec-Jan.	• Malodorous (when exposed) 'rotting, furred brown sludge' developed rapidly, coating gravel and forming around all cobbles/boulders in shallow, slow flowing patches; largely a combination of algae and diatoms, dominated by *Oscillatoria* ?*limosa* and naviculids, as well silt, bacteria and a rare unicellular alga, *Cosmarium* sp.
Du Toits	• Small areas of filamentous algae, dominated by common *Spirogyra* spp. (98% of sample biomass). • Assortment of unicellular algae and colonial diatoms also present; several stones coated with thin film of unicellular alga which had accumulated brown/red pigment, possibly *Haematococcus* sp. (although many unicellular algae enter a resting phase in this manner).	• Similar assemblage composition and densities as in Dec-Jan.	• A few patches of filamentous green algae apparent. • Red-brown film of periphyton (diatoms, ?*Haematococcus* and/or other unicellular algae) increased to cover much of substratum and was considerably denser on stone surfaces, especially in shallow, slow-flowing areas. • Bleached remains of desiccated periphyton on the large proportion of entirely or partially exposed cobbles and boulders.
Riviersonderend	• Small, sporadic patches dominated by *Spirogyra* spp. (95-100% of sample biomass). • Chlorophytes *Mougeotia* sp. (0.5%) and *Cladophora cf. fracta* (0.5%), and rhodophytes *Ballia* ?sp. nov. (3%) and *Compsopogon coeruleus* (0.5%) also present.	• Algal densities marginally elevated above Dec-Jan levels, but cover still < 1%. • Assemblage dominated by *Spirogyra* (48%) and *Zygogonium* (48-100%), with *Mougeotia* sp., *Ballia* sp., *Closterium* sp., *Anabaena* sp., two species of *Zygnema* and the diatom, *Navicula* sp. also present.	• Algal cover of dense mats of green filamentous algae increased to ≥ 60% of river bed. • Similar assemblage composition to early summer, but with reduced species richness; algal masses dominated by *Spirogyra* spp. (85-98% of sample biomass), with small percentages of *Zygogonium* sp. (≤ 15%), *Closterium* sp., and *Anabaena* sp. • Numerous patches of desiccated algae along margins and in elevated areas within channel.

Macrophyte senescence and decomposition

A high proportion of senescent and decomposing plant material, primarily *Isolepis digitata*, accumulated rapidly in the impacted location of the Riviersonderend during the two months when flows were experimentally reduced below long-term minima (Figure 4.9d). Although not quantified, decomposing plant material was present throughout the affected reach, concentrated in pools and other low-velocity biotopes (Section 6.3.4 and Table 6.33). Some patches of decomposed fragments of *I. digitata* remained in April, although the majority of decomposed plant matter had been transported from the reach by naturally elevated flows, following removal of the diversion weirs. Water colour changed from pale gold to dark orange-brown in isolated, non-flowing pools mid-summer, where plant decomposition was evident, as well as during April when plant leachates were eliminated from the reach. Although a slight increase in water colouration also occurred in the control location, it was with the onset of elevated flows in May and probably due to leachates in incoming water from upstream. The other two experimental sites had naturally lower densities of instream and marginal vegetation (Chapter 2), but also exhibited some evidence of accelerated decomposition of vegetation, as well as an increased presence of coarse and fine organic detritus, in low-velocity biotopes at extreme low flows (see Section 6.3.4 and Table 6.33; pers. obs.).

5.2.4 Effects of low flow regime on the overall water chemistry of sites

Following examination of the responses of single chemical variables to spatiotemporal flow patterns, the effects of different low flow regimes on the overall water chemistry of sites were investigated using PCA, with *a priori* reduction in data dimensionality (Section 3.3.2). The results are presented in Table 5.6 and Figure 5.5, with just over 69% of the variance explained by the first three principal components. Although there was little obvious separation on the basis of season or low-flow disturbance, separation of samples along PC1 and PC2 yielded three clusters (Figures 5.5a, b). The largest of these clusters (Group 1) could be further divided into two subgroups, primarily reflecting naturally higher nutrient, and somewhat lower and/or more variable anion concentrations at the Elands and Molenaars sites (1a), versus the other two sites (1b) (Table 5.6; see also Table 5.1). Further sample separation in this group along PC2 and PC3 was driven by subtler differences in [SiO_2-Si], maximum temperature, and mainstream pool O_2 levels (Table 5.6). Within subgroup 1a, any possible low-flow effects were obscured by the high chemical similarities between the two sites, in addition to natural variability among months and, to a lesser extent, between locations. Similarly, the close clustering of most Du Toits and Riviersonderend samples (as subgroup 1b; Figure 5.6) provided little evidence of flow-related effects.

Of importance was the separation out of a singleton from the Riviersonderend impact location from all other samples, including the corresponding control sample, for the post-impact phase in April (RI04, Group 2), as well as the sample trajectory evident for the impact location (Figure 5.5a). The sample had the highest negative and positive principal component scores for PC1 and PC2, respectively, thereby diverging markedly from control conditions for most variables. Further, while similar in [SiO_2-Si], anion concentrations, and

(depressed) maximum temperature and pH, to the May data (Group 3), it showed higher [inorganic-N], DO and conductivity. This result suggested a flushing out of accumulated water of a different quality from natural, coupled with the effects of a natural increase in discharge magnitude in early autumn (Figure 4.7). It also corresponded with findings based on time series and Q-C analyses above. Near natural conditions were attained by the end of the study period, as shown by the close agreement between samples RC05 and RI05 (Figures 5.5a, b).

Table 5.6 Eigenvalues, percentages of variation and eigenvectors for PC1-PC3, based on a PCA of water chemistry for all sites and locations at low flows.

	PC1	PC2	PC3
Eigenvalue	3.74	2.15	1.03
Explained variance (%)	37.4	21.5	10.3
VARIABLE			
pH	0.379	-0.258	-0.100
Conductivity	-0.398	0.211	-0.239
Anion Ratio	-0.452	-0.021	0.182
SO_4^{2-}	-0.257	-0.193	-0.277
Cation Ratio	0.061	-0.425	0.062
PO_4-P	0.427	0.148	0.064
Inorganic-N	0.483	0.123	-0.145
Log_{10} SiO_2-Si	0.081	0.468	-0.418
Pool O_2	0.037	0.215	0.785
Maximum Temperature	0.033	-0.607	-0.060

5.2.5 Comparison of short-term variations in chemistry at low flows with historical trends

Site summary statistics based on an examination of historical water chemistry records (Table 3.4) are presented in Table 5.7. The results enabled the short-term study to be placed in a disturbance history context, both in terms of natural variability in site chemistry during the dry season (Table 5.1) and the degree to which experimental conditions at low flows (Table 5.1 and Appendix 5.1) fell within or outside the range of physical and chemical conditions naturally experienced over time at each site. No historical data were available for temperature or DO, or for specific biotopes, while ammonia concentrations in the present study were below detection limits and TDS values discarded (Section 3.3.2).

For all sites, natural values for water chemistry typically were well within the ranges recorded over the past 20-30 years (Tables 5.1 and 5.7), and seldom as high as historical maxima. In the cases of Ca^{2+}, SO_4^{2-}, SiO_2-Si and nutrients, present-day values were at or occasionally below historical minima for certain sites. Specifically, Ca^{2+} concentrations approximated historical minima at the Molenaars, Elands and Riviersonderend sites, as did SO_4^{2-} in the first instance. Concentrations of SiO_2-Si were a little lower than historical minima for all sites, except the Riviersonderend. Nutrient values were similar or well below

historical minimum concentrations for the Du Toits, as well as for the Riviersonderend (only for inorganic-N). Given the short-term nature of the present study, the consistently higher variability in constituents calculated for historical data, based on comparison of CVs (Tables 5.1 and 5.7) was not unexpected. Of interest was the sole exception, SiO_2-Si, where CVs during the present study exceeded historical percentages at all sites. Historically, for December to May, pH was consistently the most conservative variable (CV = 17-19%), while greatest natural variability was found for inorganic-N, PO_4-P and Ca^{2+} (CV = 113-170%). A similar historical pattern of variability in these variables was evident for the peak of the dry season (Feb-Mar), although with some CVs somewhat elevated (e.g. CV_{max} of 228% for inorganic-N, Du Toits site; Table 5.7).

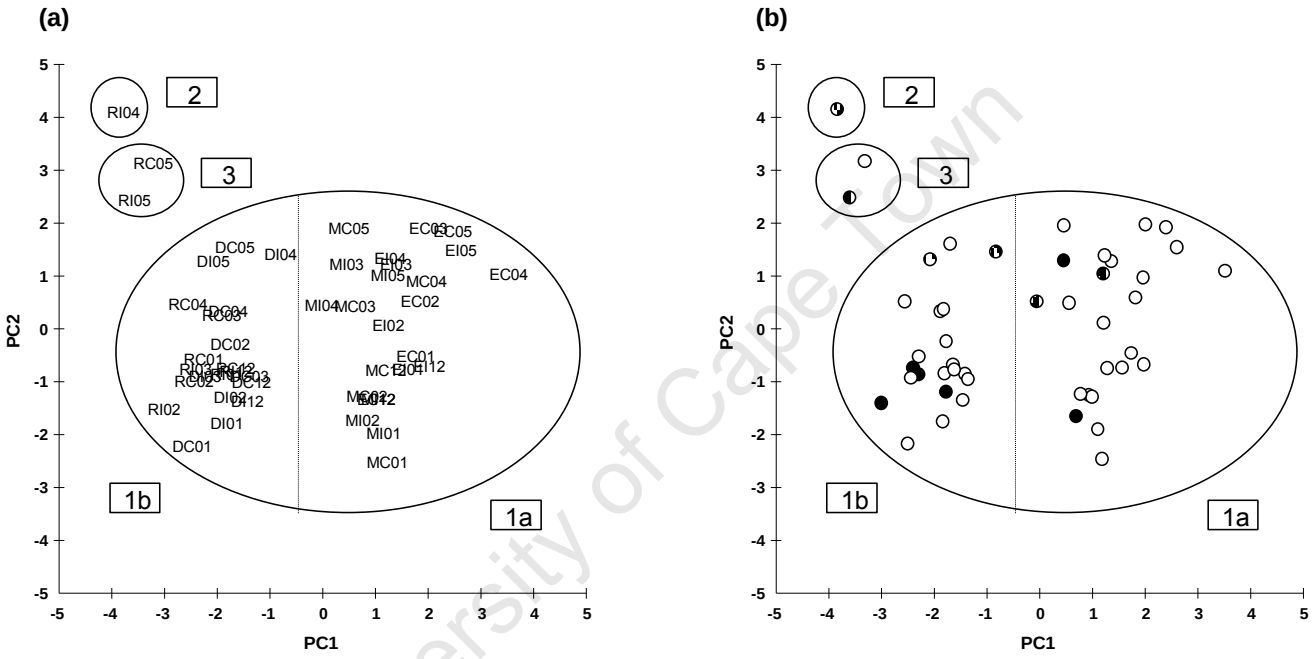


Figure 5.5 **(a) Loadings of monthly water chemistry samples, for each site and location, on PC1 and PC2.** Three major groups are delimited by ellipses, while a dashed line denotes further separation among samples within group 1 (1a and 1b). E = Elands; M = Molenaars; D = Du Toits; R = Riviersonderend; C = control location; I = impact location; 12 = Dec; 01 = Jan; 02 = Feb; 03 = Mar; 04 = Apr; 05 = May. **(b) Representation of the same PCA output, differentiating among samples collected at natural low flows (open circles), extreme low flows (solid circles), and those from flow-impacted reaches following reinstatement of natural flows (shaded circles).**

Comparison of historical chemical ranges for February-March with data collected from flow disturbed locations showed that chemistry values for such reaches remained well within historical ranges (and still often close to minima; Tables 5.1 and 5.7, and Appendix 5.1). Variables that fell below historical minima under natural low flows showed the same tendency at abnormally low discharges.

Table 5.7 **Summary statistics for historical water chemistry records for each site for (a) the temporal window matching the present study (December-May), and (b) the months (February-March) corresponding with the impact phase.** Long-term data are available for 14 of the variables measured in this study. No. Rec. = number of records for each variable. Units of measurement differ from those of the present study, and are indicated below. Units: Conductivity (mS m^{-1}); TDS (mg ℓ^{-1}); pH (units); Alkalinity (mg ℓ^{-1} of $CaCO_3$); anions, cations and silicon (mg ℓ^{-1}); nutrients (mg ℓ^{-1} N or P). *Inorganic-N represents NO_2-N + NO_3-N.

SITE	(a) HISTORICAL STATISTICS FOR STUDY MONTHS (DEC-MAY)							(b) HISTORICAL STATISTICS FOR IMPACT MONTHS (FEB-MAR)						
VARIABLE	NO. REC.	MEAN	± SD	CV (%)	MEDIAN	MIN	MAX	NO. REC.	MEAN	± SD	CV (%)	MEDIAN	MIN	MAX
ELANDS														
Conductivity	376	3.85	2.02	53	3.50	1.30	26.50	121	4.09	2.94	72	3.60	1.30	26.50
TDS	329	22.76	9.75	43	21.00	9.00	136.00	104	23.82	13.85	58	21.00	11.00	136.00
pH	375	5.25	0.96	18	5.00	3.22	9.05	120	5.28	0.89	17	5.07	3.72	8.24
Alkalinity	345	6.096	4.961	81	5.300	0.100	63.100	110	6.844	7.142	104	5.400	0.900	63.100
Na^+	338	3.366	1.900	56	3.200	0.900	33.000	108	3.560	2.974	84	3.200	1.300	33.000
K^+	334	0.452	0.467	103	0.330	0.010	5.140	106	0.506	0.606	120	0.340	0.030	5.140
Mg^{2+}	328	0.643	0.478	74	0.550	0.100	6.700	104	0.684	0.688	101	0.600	0.100	6.700
Ca^{2+}	311	1.094	1.632	149	0.800	0.100	20.700	100	1.349	2.479	184	0.800	0.100	20.700
$C\ell^-$	338	5.915	3.406	58	5.600	0.700	56.900	108	6.146	5.374	87	5.550	0.700	56.900
SO_4^{2-}	313	4.060	2.922	72	3.200	0.100	22.600	101	3.821	3.245	85	2.900	0.100	22.600
PO_4-P	320	0.022	0.034	157	0.014	0.001	0.464	98	0.025	0.055	224	0.012	0.001	0.464
*Inorganic-N	306	0.121	0.132	110	0.070	0.010	0.900	101	0.148	0.167	113	0.080	0.010	0.900
NH_4-N	324	0.065	0.095	146	0.050	0.004	1.150	104	0.063	0.108	171	0.050	0.004	1.110
SiO_2-Si	337	2.774	1.097	40	2.910	0.290	8.850	107	3.278	1.243	38	3.350	0.660	8.850
MOLENAARS														
Conductivity	505	4.14	2.24	54	3.90	0.90	38.60	168	4.10	1.74	42	3.90	0.90	22.20
TDS	456	25.05	6.60	26	24.00	12.00	58.00	151	24.95	5.63	23	24.00	13.00	43.00
pH	503	5.85	1.01	17	5.84	3.65	8.70	167	5.94	0.99	17	6.00	3.95	8.28
Alkalinity	474	6.676	4.344	65	6.050	0.400	62.100	159	6.842	5.539	81	5.900	0.800	62.100
Na^+	465	3.909	0.948	24	3.900	1.100	13.100	155	4.070	0.993	24	4.100	1.900	13.100
K^+	460	0.623	0.410	66	0.530	0.010	2.780	154	0.679	0.457	67	0.540	0.010	2.730
Mg^{2+}	459	0.711	0.362	51	0.600	0.100	2.600	153	0.708	0.396	56	0.600	0.100	2.600
Ca^{2+}	436	1.231	1.390	113	1.000	0.100	22.200	147	1.301	1.897	146	1.000	0.100	22.200
$C\ell^-$	465	6.344	2.046	32	6.200	1.500	29.200	155	6.443	2.641	41	6.300	1.500	29.200
SO_4^{2-}	443	4.130	2.628	64	3.500	0.100	16.600	151	3.857	2.274	59	3.300	0.100	10.700
PO_4-P	450	0.017	0.015	88	0.014	0.001	0.115	148	0.017	0.016	98	0.013	0.001	0.109
*Inorganic-N	433	0.102	0.083	81	0.084	0.010	0.560	149	0.109	0.088	81	0.105	0.010	0.450
NH_4-N	450	0.047	0.045	96	0.040	0.001	0.660	149	0.050	0.058	115	0.040	0.004	0.660
SiO_2-Si	464	3.691	1.425	39	3.920	0.290	15.000	154	4.392	1.641	37	4.370	0.990	15.000

Table 5.7 Continued.

SITE	(a) HISTORICAL STATISTICS FOR STUDY MONTHS (DEC-MAY)							(b) HISTORICAL STATISTICS FOR IMPACT MONTHS (FEB-MAR)						
VARIABLE	NO. REC.	MEAN	± SD	CV (%)	MEDIAN	MIN	MAX	NO. REC.	MEAN	± SD	CV (%)	MEDIAN	MIN	MAX
DU TOITS														
Conductivity	184	4.58	1.76	38	4.00	1.30	15.00	57	4.61	1.96	43	3.90	1.30	12.80
TDS	123	24.72	7.39	30	23.00	5.00	55.00	41	24.02	6.84	28	23.00	14.00	50.00
pH	131	4.90	0.94	19	4.60	1.83	7.80	43	5.05	0.89	18	4.85	3.13	7.00
Alkalinity	123	4.680	3.302	71	4.100	0.100	15.600	41	4.873	3.475	71	4.400	0.500	15.600
Na^+	129	4.692	1.113	24	4.600	0.500	8.100	42	4.621	0.905	20	4.600	2.700	7.100
K^+	124	0.376	0.323	86	0.310	0.020	2.810	39	0.313	0.190	61	0.290	0.060	0.900
Mg^{2+}	126	0.919	0.437	48	0.800	0.100	2.900	42	0.905	0.473	52	0.800	0.100	2.900
Ca^{2+}	119	1.014	0.926	91	0.800	0.100	7.900	42	0.986	1.248	127	0.750	0.100	7.900
$C\ell^-$	129	9.001	2.434	27	8.500	2.500	18.000	42	8.681	2.354	27	8.550	3.500	13.900
SO_4^{2-}	120	3.305	2.519	76	2.900	0.100	12.800	40	2.800	2.273	81	2.450	0.100	11.000
PO_4-P	116	0.013	0.017	128	0.010	0.001	0.157	36	0.014	0.025	177	0.010	0.002	0.157
*Inorganic-N	108	0.048	0.080	169	0.020	0.001	0.690	36	0.049	0.112	228	0.020	0.010	0.690
NH_4-N	120	0.056	0.042	76	0.050	0.010	0.230	39	0.056	0.044	78	0.050	0.010	0.180
SiO_2-Si	128	2.266	0.817	36	2.455	0.230	4.180	42	2.500	0.726	29	2.555	0.380	4.180
RIVIERSONDEREND														
Conductivity	191	4.43	2.63	59	3.90	2.00	34.40	62	4.32	1.37	32	4.00	2.40	9.60
TDS	127	23.70	8.28	35	23.00	11.00	59.00	43	22.95	7.93	35	22.00	12.00	48.00
pH	133	4.73	0.92	19	4.50	1.88	8.20	46	4.84	0.96	20	4.57	3.04	8.20
Alkalinity	127	4.837	3.771	78	4.000	0.100	17.800	43	4.763	4.040	85	4.500	0.100	17.800
Na^+	131	4.187	1.499	36	4.000	2.000	12.700	45	4.256	1.211	28	4.000	2.600	8.000
K^+	128	0.355	0.236	66	0.285	0.010	1.400	43	0.358	0.252	70	0.280	0.010	1.120
Mg^{2+}	129	0.950	0.591	62	0.900	0.100	4.900	45	0.938	0.497	53	0.900	0.100	2.600
Ca^{2+}	116	1.062	1.049	99	0.850	0.100	7.300	40	1.208	1.312	109	0.900	0.100	7.300
$C\ell^-$	131	8.209	2.864	35	7.800	1.900	22.600	45	8.109	2.481	31	8.300	3.700	15.500
SO_4^{2-}	123	3.468	2.619	76	3.200	0.100	16.900	41	3.256	2.297	71	3.000	0.100	9.700
PO_4-P	124	0.014	0.013	94	0.012	0.001	0.125	43	0.014	0.019	135	0.010	0.001	0.125
*Inorganic-N	100	0.039	0.066	170	0.020	0.003	0.380	36	0.028	0.028	101	0.020	0.003	0.120
NH_4-N	119	0.059	0.057	97	0.048	0.010	0.400	41	0.068	0.080	117	0.040	0.010	0.400
SiO_2-Si	129	1.565	0.793	51	1.570	0.070	3.210	44	1.765	0.725	41	1.725	0.120	3.210

5.3 DISCUSSION

5.3.1 Direct effects of low flow regime on water chemistry

An examination of short-term, spatiotemporal variations in physical attributes and chemical constituents, linked directly to natural and unnatural alterations in low flow, yielded few discernible consistent impacts of discharge reduction on water quality. The lack of marked changes in chemistry was despite manipulated reductions in discharge magnitude to below historical minima at locations within all experimental sites, and for unnatural durations of approximately two months coincident with the peak dry season (Chapter 4). Trends in most individual chemical constituents proved weak to non-existent or difficult to ascertain conclusively, on the basis of time series analysis, summary statistics or Q-C relationships, over the discharge range encountered. A number of studies of the effects on water quality of experimentally reduced discharges (e.g. Kraft 1972; Rader and Belish 1999; Dewson *et al*. 2007a, b; McIntosh *et al*. 2008), regulated flows (e.g. Lillehammer and Saltveit 1984b; Cazaubon and Giudicelli 1999), and naturally very low and drought flows (e.g. Biggs and Close 1989; Caruso 2000) have had similarly limited outcomes for various variables. Further, similarly weak or inconsistent relationships for chemical variables were also reported by Malan and Day (2002a) with increasing discharge (Section 5.1.1).

Natural spatiotemporal variability in chemistry at low flows

Even though water quality was broadly similar across the study reaches overall (Chapter 2), the chemical character of individual sites or site subgroups differed significantly for more than half the chemical constituents examined (particularly for nutrients). Specific information on within-site variability, gleaned from the two locations on the control river, still proved indispensable in discriminating between short-term, natural stochasticity and potential responses to manipulated flow disturbances. Where site-specific differences were evident, relationships between discharge and a particular chemical constituent were not necessarily consistent throughout, highlighting the additional importance of having a control location within each experimental site.

Net patterns of natural variability however limited, sometimes obscured subtle or short-duration changes in water chemistry in relation to natural peak dry season or extreme low flows. The potential influence of such variability on the outcomes of studies of the effects of low flows on water chemistry has been acknowledged, but interestingly, seldom explicitly incorporated as a contributing factor. In contrast, in hydrological studies variability is often acknowledged as a key discriminatory criterion (Poff and Ward 1989; Biggs *et al.* 1990; Richter *et al.* 1996, 1997a; and Poff *et al.* 1997). Of all sites, the Molenaars as the largest river, and representing a foothill zone, showed greatest internal stability in water chemistry at low flows. This suggested that the other upper-reach sites might be expected to experience a greater natural disturbance

regime in terms of water quality, possibly in concert with more variable dry-season flow patterns in certain cases (Chapter 4). Implications of such differences in disturbance history are discussed further in Chapter 8.

Month-to-month differences in the concentrations of most chemical variables tended to be fairly low, and supported by weak relationships with discharge magnitude, suggesting a measure of dry season stability. This was particularly evident for dissolved oxygen (in riffles and runs) and some salts (e.g. sodium, magnesium, chloride). In contrast, a few variables, among them silicon, calcium, and some nutrients, naturally fluctuated widely over time, weakening discharge-related relationships. Although such variations were marked across the sites (and supported by historical data for the last two variables) they were probably slight at a regional scale. Only a few of the variables sampled, particularly conductivity, showed natural consistent increases with flow reduction to its lowest levels midsummer. As expected, the main changes in water chemistry occurred at the end of the dry season, with the initiation of a natural climatic shift to autumn conditions coupled with elevated discharges (Chapter 4).

Effects of extreme low flows

Short-term, manipulated reductions in discharge to well below natural flows resulted in few detectable water quality impacts. Where flow-related changes in physical and chemical variables were in evidence, they were typically minor and still of the same order as those occurring naturally in the dry season. Moreover, as was the case with natural responses in chemical variables to low discharges, the observed responses to abnormal flow reductions were not necessarily consistent across all rivers. Similar findings have emanated from other studies addressing the effects of discharge reductions on water quality (Section 5.1). For instance, among three perennial New Zealand streams of differing baseline water quality, with short-term but severe experimental discharge reductions changes in conductivity, pH, temperature and dissolved oxygen were often limited, inconsistent and not necessarily proportional to the magnitude or duration of flow diversion (Dewson *et al*. 2007a, b; James *et al.* 2008, 2009). The authors acknowledged, however, that physicochemical variables were not measured in the first three days immediately following flow manipulation, and that lengthier periods of low flow might have led to more pronounced impacts (Dewson *et al*. 2007b). Differences in trends also likely reflected differences in the baseline water quality of individual sites, especially with respect to the extent of anthropogenic effects (Death *et al*. 2009).

In the current study, electrical conductivity was one of few variables clearly responsive to extreme low flows, particularly in the most experimentally flow-altered reach and the least flow-altered, but most anthropogenically modified river. As anticipated, the direction of change in conductivity at unnaturally low flows (negative) was the same as under natural midsummer conditions, but amplified. The increase in conductivity was particularly evident in isolated pools previously linked within the main channel, in the reach subjected to the most dramatic discharge reduction. It reached 112% above only marginally elevated mainstream values recorded for still-flowing areas of the impacted channel. Shifts in the concentrations of most major ions at low flows (e.g. K^+, SO_4^{2-}) probably were cumulatively principally responsible for these

responses of EC to discharge. Malan and Day (2002a), in an analysis of discharge-concentration trends for South African rivers, found that such conservative variables showed the most consistent and reliable relationships with flow. Local ecotoxicological tests have defined EC concentration-ecological response relationships for indigenous invertebrates, including *Afronurus barnardi* (Heptageniidae) and *Tricorythus discolor* (Tricorythidae) from the Molenaars and Breede rivers, respectively, with sodium chloride as the toxicant (Scherman *et al.* 2003). Toxicology results placed elevated conductivity values of the magnitude recorded in this study (max = 7.15 mS m^{-1}) immediately below reference (natural) conditions, with only marginal potential for short-term chronic toxicity.

The elevated conductivities were anticipated and could be attributed to a combination of factors linked most directly to changes in physical habitat (Lake 2000; Malan and Day 2002b). Perhaps most importantly, extreme flow reduction severed physical connections with the flowing section of the main channel (Chapter 6), and thus links with water of naturally low conductivity from upstream (the control location and reach above it). It also generated dramatic changes in the proportions and hydraulics of standing and slow-flowing biotopes (Chapter 6). Evaporation of standing water in the isolated pools and hence, concentration of salts, during the hot summer months further contributed to the observed trend. Evaporation has been shown to have a significant and rapid effect on conductivity in perennial rivers, increasing concentration within as little as 24 hours (Dallas *et al.* 1998).

Increased conductivity with flow reduction was consistent with the majority of published studies addressing this constituent (e.g. Anderson and McCall 1968; Pollard *et al.* 1996; Rader and Belish 1999; Malan and Day 2002b; Caruso 2002; Dewson *et al*. 2003; Section 5.1.1). Even during natural lowest-flow periods, for example, for seven of nine New Zealand rivers studied, Biggs and Close (1989) found that conductivity (and concentrations of major ions) were significantly negatively correlated with average daily discharge. With the most severe drought on record in the perennial South African Sabie River, conductivities and temperatures in persistent pools generally increased with time, as did pH values, over the period of extreme low flows, as pool volumes declined and water evaporated (Pollard *et al.* 1996). Car (1983) reported increases in the same variables (conductivity, temperature and pH) and also in pools, with an experimental reduction in water level of 54% in the Orange River, South Africa; figures were within the tolerance range of the dominant invertebrate, *Simulium chutteri*. Dramatically reduced discharges during a lengthy (5 y) drought period resulted in unnaturally elevated concentrations of dissolved solids in four rivers in New Jersey, U.S.A. (Anderson and McCall 1968). Also, Caruso (2002) showed that as a result of extreme low flows at 12 river sites across the Otago Region of South Island, New Zealand, induced by a one-year drought, conductivity was sharply elevated above baseline concentrations, due to decreased dilution at very low discharges and increased evaporation (coupled with groundwater inputs).

As in the current study, for four New Zealand streams routine reductions in mean annual low flow, ranging from only 28 to 98% below abstraction points, led to elevated downstream spot conductivities in all instances

(cf. upstream sites), but no consistent changes in pH (Dewson *et al*. 2003). In contrast, experimental, short-term discharge reductions of 50 to 75%, in experimental streamside channels in Canada, did not result in significant changes in conductivity (or in temperature, pH or DO) (James *et al.* 2008). Conductivity was also largely unaltered by experimental discharge reduction in three perennial, small New Zealand streams: the clean-water Reef Creek, mildly polluted Kiriwhakapapa Stream, and moderately polluted Booths Creek (Dewson *et al*. 2007a, b). While a small increase in conductivity was detected soon after discharge reduction by more than 90% for a month in Kiriwhakapapa Stream, no change in EC was apparent in the two other streams subjected to similar magnitude and duration flow perturbations (Dewson *et al*. 2007b; James *et al.* 2008). With extended major (> 90%) flow reduction for a similar duration to that of the present study (i.e. two months; James *et al.* 2009) and over the subsequent year (Dewson *et al*. 2007a), there was a significant, but small conductivity increase in the most natural stream, Reef Creek. Though not explored, the possible role of groundwater recharge/discharge contributions in influencing conductivities (and other aspects of instream condition; e.g. Moon 1956) at such very low surface flows could not be discounted (e.g. Clinton *et al*. 1996; Rader and Belish 1999; Caruso 2002; Dahm *et al.* 2003). In temporary systems, increases in ionic concentrations with drying have sometimes lead to altered pH (Williams 1996), but in the present study pH remained stable.

A definitive overall relationship between dissolved oxygen and discharge was not evident in this study, as also found by Malan and Day (2002a) for multiple South African rivers. The observed within-reach variability was also unsurprising, given the recognised short temporal scales of variation in this chemical constituent, the natural hydraulic variability of biotope patches, and the influence of other factors (e.g. plant photosynthesis-respiration cycles) (Gordon *et al*. 1992; Dallas and Day 1993; Williams 1996; Caruso 2000;). In a similar experimental study of three New Zealand streams, dissolved oxygen also was largely unaltered by manipulated discharge reduction greater than 89%, though it was noted that nocturnal concentrations might have been marked (Dewson *et al*. 2007a). There was a small, significant decline in DO concentrations in the two most flow impacted sites, Booths and Reef creeks, however, immediately following one month of flow reduction (Dewson *et al*. 2007b). Further, DO reductions (but not to abnormally low levels; James *et al.* 2008) were recorded in the former stream after two months (James *et al.* 2009) and in the latter stream after a full year (Dewson *et al*. 2007a) of continued artificially lowered flows.

Significant differences in DO with biotope type were found in the present study. The result underscored possible longer-term implications on invertebrate distribution patterns of biotope-specific water quality patterns under protracted low flows, a thus far largely unexplored topic in perennial rivers. Pools exhibited far lower and more variable oxygen levels than runs or riffles, probably due to the well-established secondary influence of velocity, depth and turbulence on O_2 concentrations (Robson *et al*. 1999; Gordon *et al*. 1992). Although the role of individual habitat or biotope features in rivers on local oxygen balance has not been well studied, according to Harper and Everard (1998), they also noted an influence of biotope type and hydraulic character on oxygen levels. Stehr and Branson (1938) found that although dissolved oxygen

levels were generally higher in riffles than pools in the small, naturally intermittent stream, Rock Riffle, U.S.A., differences in DO among pools and from riffle to riffle were as great as the inter-biotope differences across seasons, when the shallow waters were flowing and well aerated; thus, oxygen content was not considered a limiting factor in the movements of invertebrates between biotopes. With the development of intermittent conditions, resulting in a partially dry streambed with isolated pools, however, DO levels declined (and carbon-dioxide levels increased) well below average flowing-water values for both riffles and pools (Stehr and Branson 1938); concurrently, water temperatures in the remnant pools also increased to well above typical stream values.

In the present study, oxygen levels were similarly low in pools at natural and extreme low flows, and irrespective of the degree of pool isolation. Drought-induced zero-flow periods in the naturally perennial Sabie-Sand River system, South Africa, resulted in decreased oxygen levels in isolated pools in comparison with near-100% saturation levels during flowing periods, but very low concentrations only became apparent in most pool refuges during the final drying phase (Weeks *et al*. 1996; Pollard *et al.* 1996). In some pools, massive algal blooms acted as oxygen pumps to replenish oxygen levels during the day (see also below), and also provided cover, both important factors in maintaining diverse invertebrate assemblages for some time under the severe low flows (Pollard *et al.* 1996). A protracted drought that caused extreme flow reduction and drying in an occasionally late-summer intermittent tributary of the Salt Fork of the Vermilion River, U.S.A., also resulted in a loss of well-oxygenated water to pool and riffle areas with their gradual isolation and exposure (Larimore *et al*. 1959). Feminella (1996) observed though, that where there were still extensive surface flow connections to adjacent riffles, oxygen concentrations (and water temperatures) in isolated pools of intermittent streams of the upper Coosa River, U.S.A., were no more variable than values in pools in more permanent streams.

Despite evidence from diverse sources of temperature increases with flow reduction to very low levels (e.g. Stehr and Branson 1938; Larimore *et al*. 1959; Extence 1981; Cowx *et al*. 1984; McElravy *et al.* 1989; Petts and Bickerton 1994; Pollard *et al.* 1996; Dallas 1998; Cazaubon and Giudicelli 1999; Rader and Belish 1999; Caruso 2002; Dewson *et al*. 2007b; Section 5.1.1), in the present case the only detectable, limited increase in instantaneous temperature occurred with the onset of natural summer conditions. Moreover, temperatures were consistent across different biotopes (cf. e.g. Stehr and Branson 1938). Flow reduction by more than 89% for one month in three New Zealand streams also resulted in limited, and variable, changes in water temperatures from ambient conditions (Dewson *et al*. 2007b), though further changes in temperature occurred when low flows were extended for another month (James *et al.* 2009) and over a full year (Dewson *et al*. 2007a). Though there were significant increases in both maximum daily temperature and temperature range after one month of severe (80%) flow reduction in Kiriwhakapapa Stream, greater flow diversion in Booths Creek (95%) had no significant effect on either measure (Dewson *et al*. 2007b); data limitations precluded the same analysis for Reef Creek. With a further month of severe flows, mean daily temperatures were significantly lowered at all sites, but not significantly so in the case of Reef Creek, an unanticipated

result possibly due to the cooling effect of groundwater (Dewson *et al*. 2007a). Maximum daily temperatures also declined detectably in all flow-altered reaches, and daily temperature range decreased (cf. the opposite trend after only a month) in two of the three reaches, both by up to > 1 ◦C (Dewson *et al*. 2007a; James *et al*. 2009).

In the current study, there were also no conclusive effects of very low flows on other variables, such as pH or alkalinity (but see Section 5.1.1, for examples of positive or negative trends reported elsewhere for multiple parameters). It proved especially difficult to unravel any consistent effects of extreme low flows on nutrient concentrations, probably in this instance in part the result of their localised interrelationships with instream vegetation (Dallas and Day 1993; Malan and Day 2002a, b), discussed below. Similarly complex trends in discharge-nutrient relationships, largely attributed to the various complex processes involved in instream nutrient cycling, are widely reported in the literature (Lake 2000; Malan and Day 2000a, b; Dewson *et al.* 2007c; see also Section 5.1.1).

Overall effects of low flows on water quality

A multivariate assessment of the potential for cumulative and/or synergistic effects of low flows on overall water quality, using principal components analysis, revealed minimal evidence of short-term effects of artificially reduced flows. The ordination sequence of samples through the various flow phases, from natural to during impact and then post-impact, for the reach in which flows were most reduced (by approx. 86%), however, showed evidence of an accumulation of degraded quality water at extreme flows. The impact only became apparent with flushing of the affected reach with reinstatement of natural, higher flows (see below). Acknowledged sampling limitations, as well as the paucity of conclusive results from an examination of both spatiotemporal and discharge-concentration trends, restricted the significance that could be attributed to this finding.

In one of few studies available for at least broad comparison, Boulton and Lake (1990) analysed sequential changes in stream physicochemistry (using 13-17 variables) associated with five different flow phases, for pool and riffle habitats, at sites on the intermittent Australian Werribee and Lerderderg rivers. According to Boulton and Lake (1990), although such physicochemically discrete phases and low flow effects were for temporary systems, similar flow-water quality relationships might also pertain to perennial rivers. Principal components analysis showed that each of the flow phases (viz. pre-flow, early flow, main flow, diminishing flow, post-flow) was characterized by a complex combination of physicochemical features. Moreover, with flow reduction during a year of drought (1982), and particularly when pools were drying up, riffle water temperatures increased, conductivities were generally elevated, and DO levels rarely approached saturation. The ‘diminishing flow’ phase was characterized by increasing water temperature and conductivity, and declining DO levels and pH.

Harrison (1966), for the naturally seasonal Munwahuku Stream, Zimbabwe (then Rhodesia), showed that conductivity (and potassium, calcium, and magnesium) and pH increased from baseline winter-dry season values, with two drying events of differing severity (runs dry for 3, or > 8 mo; pools retaining small amounts of stagnant water, or dry for 1-6 mo), and then decreased again with re-flooding; temperatures in desiccating pools also exceeded the mid-summer maximum. Chlorides, in contrast, decreased during the drying phase, while no obvious changes were measured for sodium or bicarbonates. Of all constituents, only the first two showed highest values about one week after rewetting.

Recovery from low flow impacts

Reinstatement of natural flows, in early April, effectively served to restore water quality by flushing water of degraded quality that had accumulated in non to slow-flowing areas of the main channel, as well as in isolated pools, from flow-impacted reaches. The flushing effect was demonstrated by still elevated conductivities in the flowing channel relative to natural concentrations nearly three weeks after resumption of natural flows in the most highly impacted river, the Riviersonderend. The increase in discharge to more natural levels also mobilised the majority of the desiccated and decomposed plant material and accumulated fines associated with the partial to complete drying of large areas of river bed at abnormally low flows, as well as possibly removing minor quantities of any precipitated salts (J. Day, FRU, UCT, pers. comm.). The action of elevated flows in flushing accumulated water of poor quality from the reach thus proved a vital reset mechanism for the river, resulting in recovery to near-natural water quality conditions within a month at most. Transportation of accumulated poor water quality out of the reach as a 'pulse' when flow resumes also has been reported by Boulton and Suter (1986) for intermittent rivers.

In New Zealand, following prolonged drought-imposed low flows during summer, recovery to pre-impact water quality was rapid at most locations and had occurred in all of the 12 rivers by late autumn (Caruso 2002). Reinstatement of a natural flow regime, after a drought had severely reduced flows in the Sabie-Sand River system, led to chemistry being fully reset to natural levels, according to Pollard *et al.* (1996). The period required for resetting a river to baseline chemical and physical conditions may be greater with longer duration low flow impacts. For example, Anderson and McCall (1968) reported a general deterioration in river water quality, due to abnormally low streamflows during a five-year drought, which was particularly evident in the latter part of the event and with residual effects on water quality still apparent 15 months thereafter.

Short-term low flow effects in the context of historical water quality

In terms of disturbance history, recorded natural fluctuations in water chemistry were well within the ranges recorded over the past 20-30 years in all of the study reaches. Moreover, comparison of historical ranges in water chemistry with data collected from flow-impacted locations at the experimental sites clearly demonstrated that even flow reduction below natural levels, and for extended periods during the peak of the dry season, did not alter any chemical variables beyond established background levels. This strongly

suggested that though there may have been isolated short-term effects on the biota of certain chemical variables at extreme low flows, it is probable that the benthic macroinvertebrate assemblage was sufficiently resistant to such a disturbance, as well as resilient, having been exposed to such chemical conditions at various times in the past (Section 1.4.3). It was therefore expected that the water chemistry conditions invertebrates experienced in the present study were within their limits of tolerance, despite being accompanied by discharges of considerable departures from natural magnitudes. Synergistic effects, including in relation to physical habitat changes, could of course not be discounted (Chapter 8).

Caruso (2002) statistically compared physicochemical data at extreme low flows with that for previous summers, when examining the spatiotemporal effects of summer drought on multiple New Zealand rivers. The analysis revealed a number of significant albeit short-lived effects of drought low flows on certain water quality parameters overall, or for particular regional clusters of biophysically similar stream sites. Furthermore, in instances where the temporal and spatial patterns in various constituents were similar at extreme low flows to those occurring normally, the magnitudes and durations of extreme values of these constituents were found to increase; Caruso (2002) noted that it is often the extreme values that most impact on the aquatic biota.

Other factors influencing water quality at low flows

In addition to the loss of habitat connectivity leading to isolated standing waters of lower quality and some differences in chemistry among biotopes with differing hydraulic conditions (Chapter 6), a couple of other biophysical responses to discharge reduction were noteworthy. These indirect consequences of extreme low flows which resulted from interrelationships between flow-mediated hydraulics, chemistry and vegetation are perhaps of as much significance as the direct relationships between discharge and chemistry discussed above, in that they may themselves have further altered water chemistry or resource availability for benthos in the affected reaches.

No major increases or decreases in nutrients were detected at very low flows and nutrient-discharge relationships lacked consistency. Observed changes in algae and macrophytes pointed to at least localised dynamics between discharge and nutrient uptake/release by vegetation though, as nutrient processing became increasingly dependent on local conditions with streambed fragmentation (Lake 2003). Phosphates and nitrates are known to be often rapidly taken up by algae and aquatic macrophytes, reducing instream concentrations (Dallas *et al*. 1994). For instance, Caruso (2002) partly attributed the typically low TP and TN concentrations, in a group of drought-impacted New Zealand streams, to their higher consumption with increased growth in macrophytes and algae. Conversely, the accumulation, death and decomposition of vegetation at extreme low flows, and the leachates from such processes, can lead to marked changes to local nutrient and detrital dynamics (e.g. decaying organic material may be a site for denitrification), oxygen concentrations, and faunal composition (Moon 1956; Armitage 1984; Pringle *et al*. 1988; Williams 1996; Malan and Day 2002b).

Algal assemblages were found to be particularly useful indicators of both natural and artificial low flow conditions, in the latter case arguably more so than water chemistry *per se*. Increases in algal incidence and densities, and shifts in assemblage composition occurred in all reaches affected by flow reduction below historical natural minima. Algal masses were prevalent in all biotopes, except the very few remaining small, higher-velocity patches, with particularly marked increases in cover in runs and pools. The proliferation of algae was most pronounced in slow- to non-flowing areas of the site subjected to greatest flow diversion, this despite its oligotrophic nature. There was an increase from natural more species-rich cover below 1% to a situation where at least 60% of the river bed was covered by dense mats of filamentous Chlorophyta, dominated by *Spirogyra* spp. In the other location subjected to extremely reduced flows (also naturally with low nutrient concentrations), the densities of periphyton, dominated by unicellular algae and diatoms, were noticeably elevated above natural levels with extreme flow reduction, with vast areas of the substratum affected. Even in the least experimentally flow-impacted reach, an epilithic coat combining diatoms and algae (including an indicator of nutrient enrichment, *Oscillatoria*) was common at extreme low flows, proliferating rapidly. The same kind of algal-diatom assemblage was not evident at naturally reduced discharges.

Numerous authors have remarked on discharge reduction or related habitat loss stimulating similar algal responses in biomass and species composition, particularly during the dry season (e.g. Moon 1956; Fisher *et al*. 1982; Armitage 1984; Biggs and Close 1989; Peterson and Stevenson 1992; Cazaubon and Giudicelli 1999; Davies *et al*. 2000; Lake 2000; Suren *et al*. 2003). Unfortunately, the extent to which algal blooms were commensurate with proportional decreases in discharge, wetted habitat, or the availability of other resources was seldom assessed (but see, e.g. Suren *et al*. 2003). In contrast with this common finding, studies of experimental flow reduction, of over 89% and for one or two months' duration, in three variously anthropogenically altered New Zealand streams showed no change in algal biomass (periphyton, as chlorophyll *a*) (Dewson *et al*. 2007b; James *et al.* 2009; see also Section 5.1). Kinzie *et al*. (2006, cited in Dewson *et al*. 2007c) was one of few studies showing decreased benthic algal biomass at severely low flows, due to insufficient water availability.

Although causal relationships between periphyton biomass and nutrients observed proved difficult to establish in a study of nine southern New Zealand rivers, Biggs and Close (1989) showed that periphyton was able respond to available nutrients only under low, stable flow regimes; chlorophyll *a* and ash-free dry weight values for periphyton biomass decreased with increasing discharge, and biomass maxima only occurred during extended periods of low flow. Flow stability at very low flows, downstream of a dam on the Durance River, France, induced the proliferation of filamentous Chlorophyceae (Cazaubon and Giudicelli 1999). In a study of low flows effects on periphyton in three different stream types in Slovenia during lowest-flow periods, Smola *et al.* (1998) reported changes in periphyton species composition and biomass, including proliferations of filamentous algae and a loss of certain species, in the alpine stream, Tržiška

Bistrica, with flow reduction (and the associated decline in average velocity). While there was no marked periphyton response to low volumes of water abstraction from the lowland Dravinja Stream, the periphyton community in a section of the karstic Branica Stream subjected to very low flows and near-zero summer velocities differed from communities of other stream sections. Davies *et al*. (2000) reported increases in periphyton cover and filamentous algae at river reference sites affected by prolonged low flows associated with a five-year drought, in the Upper Murrumbidgee Catchment, Australia. Suren *et al*. (2003) showed distinct differences in periphyton communities in river runs at summer low flows in the low-enrichment Okuku and highly enriched Waipara rivers, due to differences in their nutrient status, with implications for system biophysical response to disturbance.

It is probable that the accelerated algal growth in the present study was a direct response to altered water quality, including increased local bioavailability of nutrients, in concert with altered biotope hydraulics (notably markedly reduced velocities; Chapter 6) at artificially lowered discharges; control patches did not show the same degree of increase in algae over the same time period. Filamentous algal and periphyton production, and nutrient uptake, are known to be influenced by current velocity (Biggs and Close 1989; Peterson and Stevenson 1992; Smola *et al.* 1998; Suren *et al*. 2003). Accrual of algal biomass in fast-velocity habitats tends to be lower than in slow-flowing environments, because of cell export. For example, Zygnematales (Chlorophyta) formed filamentous mats earlier and more densely in slow-flowing areas than in fast currents (Peterson and Stevenson 1992). Algal communities growing in slow currents typically also support high biomass (though with greater potential as a result for cells to become light or nutrient limited, with the latter potentially exacerbated by the low nutrient renewal rates of slow-current environments). While production generally declines overall with extremely low flow, the build-up of nutrients with raised retention times, elevation of temperatures and solar radiation can lead to isolated pools becoming "temporary hotspots of production" (Lake 2003, p. 1166) with development of dense algal growths, in turn potentially precipitating marked diel changes in oxygen concentrations (Pollard *et al.* 1996; Stanley *et al*. 1997; Ruse and Davison 2000; Dahm *et al*. 2003). For example, development of thick mats of filamentous green algae (*Cladophora*) with flow reduction in Sycamore Creek, an intermittent desert stream, U.S.A., lead to nutrient depletion and elevated levels of dissolved oxygen (Stanley *et al.* 1997). As loss of habitat connectivity occurred with progressive drying, stranding and senescence of the algal mats occurred, generating flocculent detritus (Fisher *et al*. 1982; Stanley *et al.* 1997).

The proliferation of algae observed in the current study, as well as its desiccation (often a temporary phenomenon, with some benthic algae desiccation resistant and capable of regeneration on inundation; Power *et al*. 1988; Ledger and Hildrew 2001) and decomposition on exposure, potentially further altered from natural, microhydraulics, oxygen, nutrients, organic detritus and silt. Any such effects likely changed the balance of food and refuge availability, contributing to shifts in invertebrate composition and distribution, in addition to responses brought about directly by reduced discharges. Various invertebrate taxa

have been shown to capitalize on increased nutrient availability as a result of filamentous algal growth particularly (e.g. Armitage 1978; Suren *et al*. 2003).

Suren *et al*. (2003) demonstrated, for example, that changes in invertebrate communities in the Waipara River over summer were linked to a shift in periphyton dominance, from diatoms and cyanobacteria to filamentous green algae. Changes in invertebrate communities in this nutrient enriched river were strongly correlated with the number of days at low flow. In contrast, in the low-enrichment Okuku River, there were lesser invertebrate responses to low flows. During a natural period of low flows leading to drying of a reach of the Somborne, a small English chalk stream, Moon (1956) observed the development of flocculent algal masses of *Oedogonium* in shallow, stagnant areas. With further water level decline, the algal masses became stranded and decayed, providing a vital refuge from desiccation for lotic invertebrates (e.g. tipulids, coleopterans, oligochaetes), as well as new temporary habitat and food sources for a different biotic assemblage (Moon 1956). Extence (1981), in a comparative study of environmental conditions and invertebrate communities in the River Roding, UK, preceding and during extended extreme low flows, reported altered water quality in conjunction with major physical habitat fragmentation. Changes in water quality with the summer drought included elevated water temperatures, small increases in biochemical oxygen demand (BOD), progressive siltation of the substratum, and accumulation of detritus. These chemical conditions contributed to an increase in the filamentous alga, *Cladophora glomerata*, as well as changes in invertebrate assemblage composition and even local loss of some taxa (Chapter 7). Scarsbrook and Townsend (1993) reported that thick mats of diatoms, apparent over the summer in New Zealand Kyeburn Stream, might have influenced assemblage composition, specifically reducing filter feeders. The stranding and desiccating effects on algal populations of river bed exposure with flow declines also can affect invertebrate abundances (Radford and Hartland-Rowe 1971), as was shown for ephemeropterans that used the algae as a food source in a U.S. desert stream, Sycamore Creek (Fisher *et al.* 1982).

While natural low flows (e.g. with seasonal drought) tend to inhibit detrital decomposition (Lake 2003) localised decomposition, for example, in isolated pools, may be intensified during flow reduction. In conjunction with algal proliferation, the progressive desiccation, senescence and subsequent accumulation of decomposed plant matter, especially *Isolepis digitata*, with habitat fragmentation in the most flow-disturbed Riviersonderend River, probably influenced the volume and quality of food and microhabitats available to certain invertebrate taxa. In addition to likely effects on aspects of water quality, such as nutrient dynamics, speculatively, leachates from decomposing vegetation might also have contributed to slightly depressed pH values (see also Boulton and Lake 1990, but cf. Larimore *et al.* 1959; Brooker *et al*. 1977) throughout February to April in the flow-impacted section of the river.

High levels of accumulated leaf litter have been recorded in pools during droughts, with associated microbial respiration implicated as a factor in accompanying DO declines (e.g. Larimore *et al.* 1959; Pollard *et al.* 1996). Brooker *et al*. (1977), for example, reported a substantial increase in water temperatures during the

lowest summer flows on historical record in the River Wye, Wales, that resulted in the accelerated death and decay of large stands of an aquatic macrophyte, *Ranunculus fluitans* (the growth of which had been enhanced by the prevailing conditions). Consequently, oxygen levels were markedly lowered and their diel fluctuations increased. Filamentous algae also began to proliferate under such deteriorating water quality conditions. In their study, pH (and free CO_2) showed greater variability and were elevated during periods of lowest discharge (and high macrophyte biomass), while dissolved solids and soluble organic carbon exhibited no trends.

Discolouration of waters in pools that became totally isolated following artificially reduced flows was observed in a few instances in the present study in one of the highly impacted reaches. A similar effect, attributed to leachates from decomposing vegetation in shrinking pools following flow cessation, has been reported in a number of intermittent stream studies (e.g. Larimore *et al.* 1959; Harrel and Dorris 1968; Boulton and Lake 1990). With extended flow discontinuation with drought (five months of zero surface flow, from summer into autumn), in an occasionally intermittent tributary of the Vermilion River System, U.S.A., remaining isolated pools became highly stagnant, and subject to thermal stratification with drastic temperature fluctuations (Larimore *et al*. 1959). Decomposition of accumulated leaves and other organic matter resulted in a deep brown discolouration of the water ('black water'; Larimore *et al*. 1959) and reached such an extent that BOD demand increased, with increased carbon dioxide production. As a result of this degradation in water quality, such pools became uninhabitable to lotic invertebrates, and flushing of accumulated poor quality water and detritus at higher flows was critical for the reinstatement of more natural biotic diversity. Independent laboratory study showed that water staining increased with the amount of accumulated plant material and its decomposition (with rate linked to water temperature), and that the latter process resulted in fluctuating bacterial populations, as well as (lagged) increases in dissolved oxygen demand, CO_2, pH and colour. While the leachate proved non-toxic, the oxygen demand it created was potentially lethal. In the naturally intermittent Werribee and Lerderderg rivers, Australia, as flow declined and ceased during the dry season, pools experienced increased discolouration as a result of vegetation leachates (in addition to increases, and high diel ranges, in temperatures, frequent DO declines to below 20%, and increases in acidity and conductivity; Boulton 1989; Boulton and Lake 1990, 1992b). Despite increasingly unfavourable physiochemical conditions as they shrank and dried out, such pools still represented the primary flow refuge for invertebrates (Boulton 1989).

Potential constraints on the detection of relationships between flow reduction and chemistry

The lack of many distinct effects of very low discharges on chemistry was not entirely unexpected, particularly as the physiochemical conditions in the impacted locations reflected the quality of the water moving through from undisturbed reaches upstream, comparatively more than it did any effects of localised conditions on water quality in each location. A common feature of the study reaches that indubitably contributed to the lack of significant trends between chemistry and discharge is their characteristically pure and oligotrophic waters, coupled with the absence of major pollution (Chapter 2). With such high quality

waters, chemical analyses tend to be at the limits of detection for many variables, where the slightest experimental error becomes magnified (J. Day, pers. comm.). Under such conditions it is seldom possible to be sure that the variability is actually in the water column and not inherent in the analysis, rendering it difficult to reliably detect minor impacts.

The short-term, localised nature of the study meant that only very marked changes in chemistry and/or over short time frames might be evident at the sites. Relationships between discharge and chemical concentrations were measured over a narrow range of flows, as compared with most other studies of flow-chemistry effects which have utilised data encompassing both high and low flow periods, often over a broader range of geographies or river ecotypes. Moreover, single, instantaneous measurements of variables were used to describe the monthly status of the majority of (but not all) constituents. Some attempt was made up front to compensate for such limitations, for instance, by employing a fairly intensive sampling strategy over a short time period and control data sets. Repeated sampling at even shorter time intervals, both during the flow reduction phase and immediately after the temporary weirs were removed, might have detected short-lived differences in water quality. Further, continuous recording would have provided clearer relationships between discharge and fluctuations in water chemistry (e.g. Dallas *et al.* 1998). Mosley (1982, cited in Caruso 2002), for example, considered that bimonthly observations might be inadequate for evaluating low flow effects on water temperature, due to the variable's marked natural spatiotemporal variability.

In a comparative analysis of variables used to measure rates of recovery from disturbance in streams, Niemi *et al.* (1993) found that the overall explanatory power of water quality variables was limited. While relatively few samples were required to reliably detect a 5% difference between variable means for reference and impacted streams for pH as a stable parameter, relatively large sample sizes were needed for DO, nitrite and nitrate. Hence, for the last variables, large sample sizes might have been required pre- and post-disturbance to detect an impact and recovery from it. Niemi *et al.* (1993) and Osenberg *et al.* (1994) noted though that the sample sizes needed for detecting disturbance effects and recovery for most biological variables assessed were even greater than those of chemical variables (Section 3.1).

The present study also focused primarily on the areas of the main channel where there was still a flow of water and constituents through the impacted reaches, albeit at really reduced rates for all experimentally disturbed locations, and thus continual replacement of any water of poorer quality. For example, Cazaubon and Giudicelli (1999) speculated that large areas of flowing riffle might function to reinvigorate water quality in a flow-regulated reach of the Durance River, France. Sampling in the flowing section of the channel additionally meant that other areas of water of altered quality, to be expected with the patchy nature of the flow disturbance effects, might not have been sampled. Also, though beyond the scope of this study, the potential influence of groundwater contributions to surface water quality patterns, of particular relevance during the dry period along such river reaches (e.g. Britton *et al.* 1993), is acknowledged.

Ecological relevance of altered water quality at low flows

Although several ecological studies at low flows have highlighted the potential for influence of altered water quality chemistry on aquatic invertebrates, it remains an area of relatively limited research (Dallas *et al.* 1994; Williams 1996; Dewson *et al.* 2007c; Death *et al.* 2009; Section 1.5.2). In this particular study, however, from a biological perspective there were likely few dramatic secondary effects of altered water chemistry at low flows on invertebrates, especially those assemblages inhabiting the flowing water sections of the main channel.

Cognisance did need to be taken, however, of changes in concentrations of select chemical variables at extremely low flows (e.g. conductivity, nutrients), as well as of key flow-related ecological processes (e.g. increased algal growth, macrophyte decay), when identifying explicit links between invertebrate response and flow-related biophysical conditions. Furthermore, some of the demonstrated differences in water chemistry among hydraulic biotopes and between flowing and fragmented, standing water areas of the channel at extremely low flows (Chapter 6) likely exerted some measure of influence on invertebrates. For instance, such flows might compel rheophilous taxa to move into less suitable patches with lower oxygen levels than those to which they are routinely exposed, such as pools, whilst obligate pool-dwellers would probably be unaffected (Chapter 7).

Within this study, the emphasis was on short-term fluctuations in water quality, in relation to a relatively narrow range of discharges within the dry season. Although subtle differences might assume greater importance in contributing to biotic response in such a context, it is uncertain as to whether a small change in a naturally stable chemical variable is more, less or as important, as a greater change in a naturally variable constituent. Moreover, there remains limited research demonstrating, for various chemical variables, what percentage of change in a particular direction at low flow is actually biologically significant. Importantly, increasing knowledge of invertebrate tolerance ranges and instream responses to changing physicochemical conditions with discharge is being generated (e.g. Dallas *et al.* 1999; Goetsch and Palmer 1997; Palmer and Scherman 1999; Scherman *et al.* 2003; Section 5.1.2).

Water chemistry was not likely to be a critical or overriding influence on the responses of benthic macroinvertebrates to low flows in the context of this study, in comparison with the direct effects of low flows (Chapter 7) and associated dynamics of physical habitat (Chapter 6). Pollard *et al.* (1996) reached a similar conclusion in a study of the biophysical effects of a drought on the perennial Sabie River, South Africa, when the river experienced the lowest discharges on record and approached flow cessation for the first time in its flow history. Towards the end of the drought, physicochemical conditions were considered extreme on the basis of most variables assessed, but water quantity and physical habitat losses together exerted a far greater impact on the invertebrate community.

Despite the main finding of only subtle changes in water quality with manipulated low flows in the present study, in Chapter 8, certain chemical variables were found to influence invertebrate assemblage composition when integrated with physical habitat factors and discharge. This highlighted the importance of considering chemistry and physical habitat together, at least in the short-term, in describing ecologically meaningful, low flow conditions.

6. PHYSICAL HABITAT DYNAMICS AT NATURAL AND EXTREME LOW FLOWS

6.1 INTRODUCTION

According to current thinking in ecohydrology, the availability and suitability of instream physical habitat in space and time are fundaments of the riverine templet that underpins biotic response to flow disturbance (Poff and Ward 1990; Section 1.4.5). Benthic community responses to flow disturbances depend on the physical complexity of the habitat (Hildrew and Giller 1994). Moreover, the biota may respond to flow alteration directly or indirectly, through a physical habitat-mediated effect (Ward 1976; Cushman 1985; Section 1.4.2, Figure 1.3). As Poff *et al.* (1996b, p. 267) emphasised "Although evidence exists that species can be adapted to the natural flow regime independently of geomorphic constraint (Lytle and Poff 2004), the *interaction* of the flow regime and geomorphic setting more precisely establishes the disturbance regime that defines the habitat template". Consequently, it is often implicitly assumed that physical habitat can effectively act as a surrogate of the flow-related needs of benthic macroinvertebrate assemblages or, more generally, river biodiversity and health (Harper and Everard 1998; Whittington 2000; Section 1.5). In order to characterize ecologically relevant low flows for invertebrates, therefore, a vital step is to develop an understanding of the ways in, and extent to, which physical habitat is directly altered with discharge reduction, at geomorphic scales of relevance to the organisms concerned (Section 1.4.7). It also allows the identification of specific abiotic measures of flow disturbance that can be most usefully linked to invertebrate response (Chapter 8). The complementary roles of higher flows in modifying physical habitat at the reach and finer scales (Petts *et al.* 1995; Sections 1.4.2 and 1.4.7), thereby ultimately altering factors such as habitat heterogeneity for biota under low flow conditions, are acknowledged for the purposes of this study.

6.1.1 General features of the relationship between physical habitat and low flows

With the fluctuations in water levels due to a changing flow regime, different river habitats expand and contract, resource availabilities shift, certain habitats become more or less isolated from others, and other physical gradients are altered as a result (Power *et al*. 1988; Stanley *et al.* 1997). While it is recognised and fairly well documented that habitat change occurs under patterns of natural and extreme (whether natural or manipulated) low flows, from reach and channel width, to hydraulic biotope and microhabitat patch scales, comparatively few studies quantify the nature of the response, and even fewer go on to make explicit the implications of such habitat dynamics for the biota (Boulton and Suter 1986; Stanley and Fisher 1992; Stanley *et al.* 1997; Tharme and King 1998; Lake 2000). Moreover, the measures of habitat change used have been a relatively small subset of the set of ecological meaningful metrics potentially available.

Empirical observations of flow-related habitat change have often been made during studies aimed simply at documenting extreme low flow impacts, such as drought, on riverine biota (Section 7.1) and typically have been largely qualitative. Arguably, the majority of quantitative information available on changes in physical habitat with flow has been simulated, as a basis for prediction of biotic response (Hawkins *et al*. 1993). As Crowder and Diplas (2000, p. 172) commented "Modeling of flow features that are important in assessing stream habitat conditions has been a long-standing interest of stream biologists." Typically, discharge-habitat relationships, many of which are non-linear (Poff *et al.* 1997; Jowett 1997, 1998), have been used to identify threshold discharges or break points below which there is a significant reduction in the availability and suitability of physical habitat for target biota (e.g. Petts and Maddock 1994; Gippel and Stewardson 1998; Lamouroux *et al*. 1998; 1999). Such relations have been developed using the kinds of multi-scale habitat modelling procedures documented in various sources, including Bovee and Milhous (1978), Nestler *et al*. (1989), Milhous *et al*. (1989), Stalnaker *et al*. (1989), Gan and McMahon (1990b), Ghanem *et al*. (1996), Hardy (1998), and Waddle (1998a), and Crowder and Diplas (2000) (see also Section 1.5).

Whether based on modelled prediction or field observation, flow reduction undeniably results in the elimination or a reduction in the quantity of wetted physical habitat, as well as changes in its hydraulic characteristics (a central aspect of quality) (Lake 2003). Reduction in habitat with declines in discharge occurs naturally in perennial rivers that exhibit flow seasonality (Sedell *et al*. 1990; Lake 2000). Moreover, it may become particularly dramatic under extreme low flows, such as those occurring during drought or in temporary systems (e.g. Hynes 1958; Larimore *et al.* 1959; Ladle and Bass 1981; Extence 1981; Cowx *et al.* 1984; Boulton and Suter 1986; Townsend 1989). As Lake (2000) summarized schematically, commencing with the exposure of marginal areas, reductions in habitat space and stream continuity (Figure 6.1, top) with low flows, especially when prolonged, may result in marked overall losses in wetted area (often coupled with a deterioration in water quality - Chapter 5), and ultimately, in organisms (Figure 6.1, bottom). Even slight decreases in discharge can result in fairly substantial reductions in wetted area that may expose river bed areas to desiccation and hence, reduce habitat availability for biota (McMahon and Finlayson 2003), particularly in shallow streams or those with naturally very low or absent dry-season flows.

Discharge alone is insufficient to describe the physical habitat impacts of very low flows, because drying is a dynamic, spatially heterogeneous process (Stanley *et al.* 1997). The "duration of time a substrate patch is within the wetted perimeter of the channel is perhaps the most important determinant of its capacity as a stream habitat" (Frissell *et al.* 1986, p. 209). Low flows may result in various patterns and degrees of spatial patchiness of aquatic habitat (Section 1.4.6), as a result of naturally dynamic cycles of expansion, contraction and fragmentation (Stanley *et al.* 1997). Reductions in reach lateral and longitudinal connectivity, breaking the stream into spatially discontinuous and continually shrinking segments or patches (Fisher *et al*. 1982), may culminate in total drying of some sections (Uys and O'Keeffe 1997b; Lake 2000; Covich *et al*. 2003), with riffles tending to desiccate more rapidly than deeper areas such as pools (Boulton and Lake 1990;

Stanley *et al*. 1997). Flow reduction may also result in pool (or other new habitat) formation, the progressive isolation of such new or existing pools, or changes in their hydraulic character, relative size, and number throughout a reach, as low flow conditions worsen or persist (Lake 2000, 2003). Pools (as well as riffles and other patch types) may fragment into smaller units and become increasingly isolated before entirely drying up, or may persist as isolated units controlled more by local than longitudinal biophysical processes (Pollard *et al*. 1996; Feminella 1996; Boulton 2003).

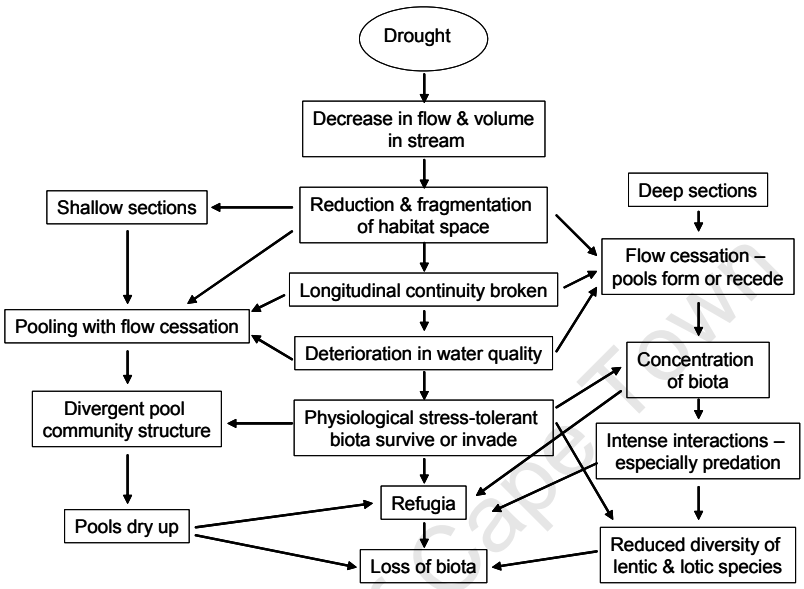


Figure 6.1 Schematic of the progressive effects of drought on stream conditions and the biota (from Lake 2000).

6.1.2 Influence of low flows on reach habitat hydraulics

Reduced flow is well understood to result in detectable changes in a range of interrelated hydraulic characteristics of rivers from reach to patch scales (Armitage and Petts 1992), with variations reflecting differences in channel morphology (general bed form and morphological units) and substratum composition (Petts *et al.* 1995; Rowntree and Wadeson 1996; Padmore 1997; Jowett 1998; Gippel and Stewardson 1998). Indeed ecohydraulics, as an area of research, is predicated on the influence on the biota of altered physical habitat hydraulics at meso- to micro-scales with changing discharge (Section 1.4.8 provides further discussion).

Use of hydraulic geometry relationships in assessing habitat dynamics at low flows

Reach relationships between hydraulic geometry and discharge provide a general description of changes in physical habitat availability with fluctuating discharge (Jowett 1997), as well as an indication of the direction and degree of expected change in associated hydraulic parameters. They have been used to indicate when mean or modal hydraulic conditions are approaching thresholds of acceptability in terms of the hydraulic

requirements of benthic macroinvertebrates, such as a minimum acceptable wetted perimeter, depth or velocity, in some instances obviating the need for more intensive habitat surveys and analyses (Tennant 1976; Stalnaker and Arnette 1976; Nelson 1980; Gordon *et al*. 1992; Jowett 1997, 1998; Gippel and Stewardson 1998). Commonly, for example, breakpoints in discharge-habitat relationships have been used to define the ecohydrological needs of the benthos, using transect-based hydraulic or habitat rating methodologies (e.g. the Wetted Perimeter method; Section 1.5 and Tharme 2003). Gippel and Stewardson (1998) pointed out, however, that although several authors consider it a valid assumption that a relationship exists between such simple measures of physical habitat and habitat suitability for target organisms (e.g. Tennant 1976; Wesche and Rechard 1980; Annear and Conder 1984; Richardson 1986), the literature provides few supporting field observations.

The hydraulic geometry of river channels may be broadly characterized using three fundamental equations (power law relationships) that relate discharge to water surface width, mean depth and mean velocity (Leopold and Maddock 1953; Tennant 1976; Bovee and Milhous 1978; Annear and Condor 1984; Stalnaker *et al*. 1989; Gordon *et al*. 1992). Hydraulic geometry relationships with discharge have been empirically explored for different streams by various researchers, but with the identification of consistent trends to some extent complicated by the site-specific nature of channel geometry, a primary determinant of such relationships (e.g. Larimore *et al*. 1959; Minshall and Winger 1968; Kraft 1972; Englund and Malmqvist 1996; Gippel and Stewardson 1998; Jowett 1998; Dewson *et al*. 2007c; see also Section 6.7). It is well established from such at-a-station discharge-hydraulic geometry relationships, that hydraulic characteristics vary with river size (and mean annual discharge; Jowett 2003) and that as discharge decreases, stream current velocity generally decreases at a faster rate and to a greater extent than water depth.

Singh and Broeren (1989), for instance, quantified the relationship between discharge, and depth and velocity, using probability distribution models based directly on field measurements. Rosgen (1994, p. 190, Figure 11) demonstrated positive trends in stream cross-sectional area, width and mean depth with increasing discharge. Jowett (1998) and Gippel and Stewardson (1998) provided examples of the use of hydraulic geometry relationships for habitat characterization with flow dynamics (see also Section 6.3). Jowett (1998) derived at-a-station regression relationships between hydraulic geometry (reach average depths and velocities) and discharge for 73 New Zealand sites with diverse hydrological regimes and physical habitat conditions. A combination of survey data from multiple cross-sections and hydraulic simulation was used; hydraulic geometry-discharge relationships for two of the streams were then compared with habitat-flow relationships modelled within IFIM. Hydraulic geometry relationships between water depth particularly, and velocity, and channel morphology were poorly developed, which rendered suppositions about habitat response to flow change difficult on this basis alone. Hydraulic geometry-discharge relationships may also be limited in that they focus on average hydraulic conditions, and typically independently on depth and velocity (Loar *et al.* 1986; Gordon *et al.* 1992; Tharme 1996; Rowntree and Wadeson 1996), thereby providing limited information on hydraulic alteration. Lamouroux and Souchon (2002) argued, however,

that simplification using average reach measures of hydraulic habitat that relate to basic hydraulic geometry was an effective alternative to increasingly sophisticated multi-dimensional hydraulic modelling.

Characterization of habitat patches and their dynamics with changing flows

For ecologically meaningful characterization of physical habitat and prediction of the effects of altered flow regimes on its availability, a more detailed meso- to micro-scale investigation of the distribution and variability of hydraulic habitat conditions within a reach is often needed (Bovee and Milhous 1978; Richardson 1986; Herricks and Braga 1987; Kellerhals and Church 1989, cited in Jowett 1998; Milhous *et al.* 1989; Tharme 1996; Rowntree and Wadeson 1996; Newson and Newson 2000). Progressively therefore, research has shifted from establishing the above simple habitat-flow relationships, to point-based analyses of habitat hydraulics across channel-spanning cross-sections, or multi-dimensionally throughout an entire reach. Furthermore, while water depth, current velocity and substratum size have remained the primary descriptors (Jowett 2003) and most conventionally measured elements (Beisal *et al.* 1998) of flow-related hydraulic habitat, more complex variables such as Froude number (Fr) and shear stress have gained prominence (Sections 1.4.8 and 8.1). In an interesting example, Lamouroux *et al*. (1992, 1995) and Lamouroux (1998) used regression-based hydraulic models to express the frequency distributions of multiple local hydraulic variables (depth, velocity, shear stress, Fr) at different discharges in river reaches, as a function of average reach characteristics, and linked the outcomes with fish habitat preferences, for the Rhône River, France (Lamouroux *et al*. 1998, 1999). Lamouroux and Souchon (2002) and others extended such flow-habitat modeling based on reach average hydraulic characteristics to fish habitat guilds, for multiple European streams and species.

Other investigations have increasingly integrated concepts from patch dynamics theory (Section 1.4.6), to examine the spatiotemporal diversity and dynamics (at transect or reach scales) of biotope, mesohabitat or functional habitat patches and the microhabitats within them (terms defined in Section 1.4.8). Notably in this regard, Waddle (1998a), Crowder and Diplas (2000) and others have advocated the use of two-dimensional hydrodynamic models to incorporate various mesohabitat features in, and generate new spatial habitat metrics for, studies of flow-related habitat suitability for lotic biota. Modelling of low flows at this scale is recognised still as a complex and experimentally error-prone area of work (Gan and McMahon 1990a).

Division of the heterogeneous riverbed landscape into smaller, more homogeneous patches, such as hydraulic biotopes or other mesohabitats, facilitates examination of complex spatial patterns at the temporal and spatial scales at which they occur (Stanley *et al.* 1997), particularly in relation to phenomena such as flow-related disturbance. In a few instances, relatively large-scale morphological features have been used to define patch units. For example, O'Neill and Abrahams (1984) used differences in river bed topography to objectively define riffle and pool units. Scarsbrook and Townsend (1993) included an explicit focus on hydraulic factors at a similar scale, defining pools as reach subsystems possessing a low water surface slope and a maximum water depth > 0.25 m, while riffles were defined as having depth maxima below 0.25 m and

water surface slopes intermediate to that of pools and cascades. Other studies have focused on finer-scale habitat patches to represent ecologically significant units for invertebrates (see Section 1.4.8), with such patches often delimited subjectively, and even compared as such across different rivers without accompanying geomorphologic or flow-related hydraulic criteria (Pringle *et al*. 1988; Jowett 1993; Newson and Newson 2000). Increasingly, such criteria and/or information on assemblage composition have been used to define different patch types, as in the illustrative examples provided below (see also Sections 6.7 and 8.1).

Hawkins *et al*. (1993) classified physical habitat at three nested levels below that of channel geomorphic unit, on the basis of various hydraulic criteria, with a first division into slow-water and fast-water channel units loosely corresponding to riffles and pools. Fast-water habitats then were subdivided into high or low turbulence classes, each with associated habitat types (turbulent rapids, riffles, etc., versus non-turbulent sheets and runs). Similarly, slow-water habitats were subdivided into two sub-levels based on pool type. Various geomorphic and hydraulic variables were used to visually differentiate fast-water and slow-water units (e.g. gradient, bed roughness, velocity, cross-section profile); the potential value of empirical validation of the hydraulic characteristics of each unit was acknowledged. Leonard and Orth (1988) calculated the proportions of riffle, run, transition and pool habitat types in three U.S. Virginian streams, for use in an assessment of the environmental flow requirements of fish from different habitat-use guilds distinguished largely on the basis of velocity. In an assessment of the relative distribution of physical habitat characteristics at four main study sites along the River Babingley, U.K., Petts *et al*. (1999) classified pool-riffle habitat into four biotope categories on the basis of hydraulic criteria, including substratum composition. Jowett (1993) used discriminant analysis to hydraulically characterize riffle, run and pool habitat types visually identified in the Ashburton River, New Zealand (Section 6.4). Froude number was used by Yu and Peters (1997) to objectively identify and classify the same three habitat types in the Platte River system, U.S.A. Comparisons of Froude number use to availability proved useful in then determining preferred habitats for 24 fish species and size classes, and in developing suitability criteria for fish species for instream flow assessment. Padmore (1997, 1998) explored in depth, the relationships among channel type, physical biotope character and diversity, and discharge magnitude for 11 rivers in northeast England known to reflect a diverse range of morphological units. Physical biotopes were identified visually in the field on the basis of dominant flow type, with different surface flow types reflecting particular combinations of hydraulics and substrata, as described in Padmore (1998, p. 27, Table 1) (see also Appendix 3.4 and Section 6.7).

Newson *et al.* (1998) reported some concurrence between such biotopes and vegetative and mineral functional habitats, based on preliminary analyses of data sets for English lowland rivers. Newson and Newson (2000) indicated that, based on habitat surveys in northeastern England, biotope-specific hydraulic geometries (i.e. using data aggregated for all pools or all riffles) might prove a useful approach for incorporating habitat scaling in addition to quality. In a study of 32 U.K. river sites, Kemp *et al*. (1999, 2000) examined the use of functional habitats as a means of effectively linking ecology with channel

geomorphology and hydrology, for river rehabilitation purposes, developing specific depth, velocity and Fr occurrence matrices for 16 different, biologically validated functional habitats. Their studies provided a link between functional habitats and biotopes, with a primary division into 'low Froude number habitats' significantly associated with only the lowest Fr class (e.g. silt, floating-leaved macrophytes) and habitats with Fr > 0.05 (e.g. cobbles) (Kemp *et al*. 2000); it was acknowledged that additional hydraulic qualifiers were necessary to further differentiate among the group of functional habitats with similarly low Fr values.

For the Truckee River, U.S.A., Kershner and Snider (1992) identified 22 habitat types at mesohabitat level, for which fish associations were documented, with microhabitat quantified as a function of individual mesohabitats (using transect-based measurements of velocity, depth, substratum and cover). Kershner *et al.* (1992) went on to identify five major functional mesohabitats (glides, main pools, lateral pools, riffles, runs) from these original types. Harper *et al*. (1992) identified 16 functional habitat types in U.K. lowland streams, on the basis of structural descriptors of vegetation and/or substratum (e.g. 'boulders/rock surfaces', 'leaf litter', 'macroalgae'), for which there were distinct invertebrate assemblages. Vadas and Orth (1998) established a mesohabitat classification system for streams and small rivers (i.e. < 50 m wide during summer), based on research conducted in the upper Roanoke River, Virginia, U.S.A., that was intended to be relevant for fish habitat use and independent of stream discharge, size or morphology (Section 6.7). Cohen *et al*. (1998) similarly identified seven mesohabitat types on the basis of channel form and hydraulic characteristics, ranging from rapids and riffles, to lateral scour pools. They recognised that such units were ecologically meaningful on the grounds of other studies, but did not explicitly address biotic composition. Their mesohabitat concept was extended to river basin scale, revealing differences in the distribution of mesohabitats within various hydro-ecoregions of the Loire Basin, France. Though Brunke *et al.* (2001) visually distinguished eight, hydraulically different mesohabitats in the River Spree, Germany, subsequent examination of their invertebrate composition revealed only three ecologically distinct mesohabitat types; mesohabitat-specific relationships between flow velocity and river discharge were used to set minimum flows (Chapter 8).

6.2 APPROACH AND OBJECTIVES

The research described in this chapter aims to deepen understanding of the nature of relationships between patterns in natural and extreme low flows and instream physical habitat, at scales of relevance to benthic macroinvertebrates. It addresses the widely held view that the availability and suitability of physical habitat are central factors underlying invertebrate response to changes in discharge, and that habitat has the potential to act as a surrogate for invertebrate flow-related needs (Section 6.1). To this end, the chapter focuses on fulfilling thesis objective 3 (Section 1.2, Figure 1.2), by addressing the related objectives to:

1) Determine the effects of different low flow regimes on the proportional availability and hydraulic character of physical habitat, from reach to channel cross-section and individual patch scales.
2) Ascertain the extent to which visually identified, hydraulically distinct habitat patches in the field

can be objectively classified as different biotope types at low flows.

3) Establish the extent to which hydraulic biotopes are robust, discrete entities independent of fluctuations in discharge magnitude and site physical character.
4) Examine biotope patch dynamics under patterns of natural and experimental extreme low flows.
5) Identify differences in the hydraulic character of various biotope types at low flows (that might represent the basis for their being inhabited by different invertebrate assemblages and taxa).
6) Determine the most discharge-responsive measures of physical habitat of potential relevance to invertebrates.

Details of methods of data collection and analysis for physical habitat are provided in Section 3.4. Within the results Sections 6.3 to 6.6, Section 6.3 explores relationships between low flows and common aspects of channel hydraulic geometry, several of which are used to indirectly represent invertebrate flow requirements at reach scale. Section 6.4 focuses on the identification and flow-related characterization of hydraulic biotopes, based on an array of hydraulic indices. As introduced in Sections 1.4.8 and 6.1, the assessment of biotope-flow relationships has been identified by several researchers as one of the more promising approaches towards characterizing the ecological flow requirements of invertebrates. Section 6.5 specifically addresses biotope patch dynamics and diversity at the reach scale, under natural and extreme low flows. Section 6.6 compares and contrasts site, location and biotope substratum conditions, as substratum composition exerts a direct influence on hydraulics (and is in turn influenced by hydraulic factors) and is a fundamental component of benthic habitat. In Section 6.7, findings are summarised and discussed alongside those of other studies that have explicitly addressed physical habitat-low flow relationships and their potential implications for invertebrate assemblages.

6.3 CHANGES IN CHANNEL-WIDTH DESCRIPTORS OF HYDRAULIC HABITAT IN RESPONSE TO LOW FLOWS

6.3.1 Relationships between wetted width and low flows

Channel profiles for riffle and run cross-sections (i.e. transect biotopes – Section 3.4.1, Figure 3.7) at each site location, illustrating wetted widths, as well as depth and velocity distributions, corresponding to a subset of instantaneous discharges (Q_{inst}) are depicted in Appendix 6.1. Corresponding stage-discharge rating curves are illustrated in Appendix 6.2. Temporal changes in wetted width with low flows for individual riffle and run cross-sections within each reach are presented in Figures 6.2a-d.

With only natural fluctuations in discharge, at the Elands control site (Figure 6.2a), channel wetted widths were similar over time, reflecting the fairly stable dry-season hydrological regime (Chapter 4). This was clearly demonstrated by run cross-sections, where there was only a slight increase to maximum wetted width (11.9 m) in May; with the inclusion of standing water, present only in February, the width of the run within

the 'impact' location (an apparent outlier at 9.2 m; Figure 6.2a) fell in line with the other run's dimensions. Riffle widths similarly varied little with flow regime (11.4-13.5 m) and were comparable to those of runs.

Wetted widths recorded in the Molenaars reach (Figure 6.2b) were the greatest of all sites, commensurate with the river's relative size and discharge (Chapter 2). Maxima naturally occurred in the highest flow month (Dec), while narrowest widths were measured at lowest discharges (Feb). Under the range of natural flows, differences in wetted widths were low at 1.3 m (9%) and 0.5 m (4%) for the run and riffle, respectively, and both transect biotopes were of similar dimensions. With a roughly 36% reduction in discharge, there was a slight increase in the absolute difference in width for the impacted run and, to a marginally greater extent, for the riffle transect (Figure 6.2b). The run decreased in width by 12.4% from maximum, to a February low of 13.3 m. Similarly, flow reduction below natural levels resulted in a loss of 2.1 m of riffle by width (a 15% decrease from maximum). Overall, however, runs showed a stronger Q-width relationship than riffle transects (see below).

In the Du Toits reach (Figure 6.2c) wetted widths were the narrowest of all sites, generally lowest in the period of lowest flows and at maxima in the highest flow month (May). Under natural conditions the control run showed limited fluctuation around 8 m width, until May when it increased by only 0.5 m. Riffles were narrower and fluctuated more in width than runs, with a greater decline of 1.9 m from maximum width to the dry season minimum of 4.8 m (Figure 6.2c). With artificial flow reduction, there was a distinct 22% decrease in run width from 6.5 m (May) to only 5.1 m (Feb). A lesser narrowing of just under half a metre was observed for the flow-impacted riffle, which meant that despite similar maxima, the riffle remained wider than the corresponding run at very low flows.

For the Riviersonderend site, at which the greatest discharge was diverted, there was a lack of consistency in maximum and minimum wetted widths in relation to month and discharge (Figure 6.2d, but see Table 6.1). Likely contributing factors were: (i) natural channel heterogeneity and the associated difficulty in classifying transect biotopes as runs or riffles; (ii) the occurrence of standing water at channel edges; and (iii) the presence of bedrock as a control on hydraulics across the impact riffle. There were marked declines in width from autumn maxima, of 2.1 m (run) and 4.0 m (riffle), with the decrease to naturally lower discharges mid-season (Figure 6.2d). Despite extreme flow reduction, run and riffle widths remained stable over the dry season at around 6.0 m and 10.7 m, respectively (Figure 6.2d). Moreover, of the two flow-impacted cross-sections, only the run demonstrated an effective doubling in width to 12.0 m with the naturally elevated discharge signaling the onset of autumn. The complex hydraulic geometry of the impact riffle, with its isolated secondary channel over bedrock, and as a result, potential for elevated experimental error, might have explained the lack of congruence with the general patterns observed at this and other sites.

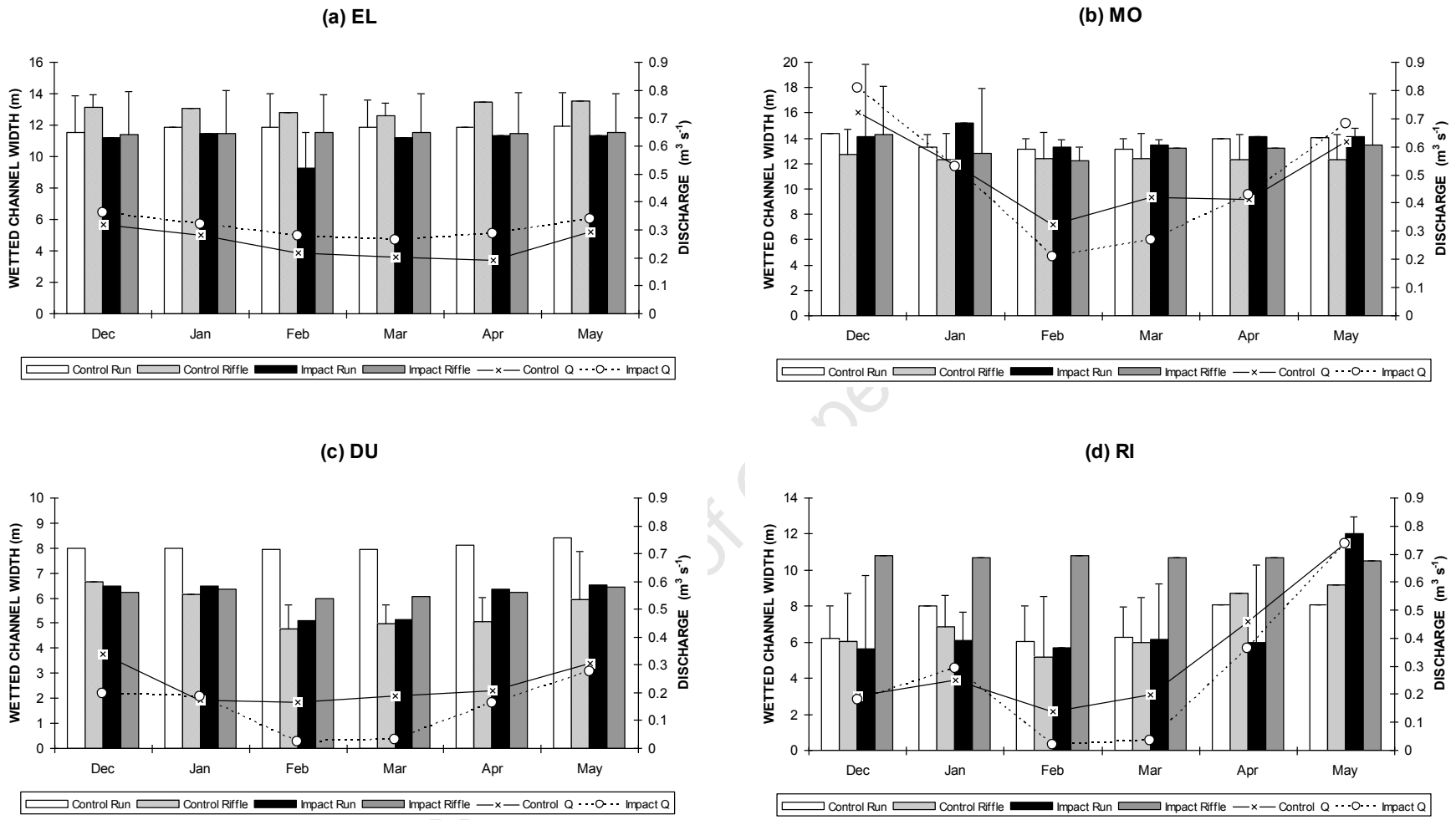


Figure 6.2 **Changes in wetted channel width with month and discharge (Q_{inst}), for run and riffle cross-sections at the sites. (a) EL - Elands; (b) MO - Molenaars; (c) DU - Du Toits; (d) RI - Riviersonderend.** Note the different scales among plots. The T bars depict the additional width represented by isolated patches of standing water along the edges of the main channel for individual cross-sections.

Analysis of direct relationships between discharge magnitude and wetted width, based on pooled cross-section data from all sites (using the ratio of width: max. width per site, vs. Q_{inst} normalised by Q_{50}), for riffles and runs combined and separately, yielded weak to imperceptible relationships (Table 6.1). This result was in large part due to the combination of data representing cross-sections of differing hydraulic geometry across reaches. Best-fit relationships (all power functions) were established when data representing standing water at the outer edges of the channel were included. As envisaged, overall there was typically a non-linear decrease in wetted width with a decrease in discharge that was weakly apparent for runs ($R^2 = 0.195$), but not discernible for riffles ($R^2 = 0.001$).

Table 6.1 Relationships between wetted channel width, including and excluding marginal patches of standing water, and discharge magnitude. The best fit of a linear, logarithmic (natural), power or exponential function is presented (R^2 - coefficient of determination). Trends of an increase (↑) or decrease (↓) in channel width with discharge reduction are indicated.

SITE AND CROSS-SECTION TYPE	*n*	WIDTH EXCLUDING STANDING WATER			WIDTH INCLUDING STANDING WATER		
		Trend with ↓ Q	Equation	R^2	Trend with ↓ Q	Equation	R^2
All sites combined							
Riffles and runs combined	96	↓	$y = 0.814x^{0.037}$	0.016	↓	$y = 0.827x^{0.058}$	0.061
Riffles	48	↑	$y = -0.022\ln(x) + 0.773$	0.014	↓	$y = 0.788x^{0.007}$	0.001
Runs	48	↓	$y = 0.870x^{0.101}$ or $y = 0.071\ln(x) + 0.876$	0.101	↓	$y = 0.868x^{0.109}$	0.195
Individual sites							
EL							
Riffles and runs combined	24	↑	$y = -1.539\ln(x) + 9.848$	0.111	↑	$y = 13.342e^{-0.109x}$	0.004
Riffles	12	↑	$y = 9.769x^{-0.175}$	0.246	↓	$y = 5.499x + 12.176$	0.417
Runs	12	↑	$y = -0.938\ln(x) + 10.183$	0.067	↑	$y = 14.541e^{-0.623x}$	0.121
MO							
Riffles and runs combined	24	↓	$y = 1.814x + 12.440$	0.167	↓	$y = 6.146x + 11.307$	0.308
Riffles	12	↓	$y = 1.799x + 11.928$	0.282	↓	$y = 6.598x + 10.732$	0.276
Runs	12	↓	$y = 14.525x^{0.062}$	0.335	↓	$y = 12.305e^{0.349x}$	0.424
DU							
Riffles and runs combined	24	↓	$y = 5.506e^{0.799x}$	0.195	↓	$y = 5.506e^{0.970x}$	0.380
Riffles	12	↓	$y = 1.283x + 5.673$	0.039	↓	$y = 5.661e^{0.546x}$	0.367
Runs	12	↓	$y = 9.565e^{0.168x}$	0.668		no standing water	
RI							
Riffles and runs combined	24	↓	$y = 6.606e^{0.494x}$	0.180	↓	$y = 1.782x + 8.643$	0.075
Riffles	12	↓	$y = 7.979e^{0.234x}$	0.040	↑	$y = -0.278\ln(x) + 9.260$	0.090
Runs	12	↓	$y = 5.468e^{0.753x}$	0.655	↓	$y = 9.904x^{0.095}$	0.299

Trends for individual sites again showed a characteristic non-linear decline in wetted width with flow reduction, except in the control case where trends were mostly absent or even weakly negative over the

narrow range of observed discharges (Table 6.1 and Figures 6.2a-d). A positive linear relationship between width and discharge was evident for control site riffles, however, especially with the inclusion of the standing water prevalent at this site (Figure 6.2a). For all sites at which flows were experimentally reduced well below naturally lowest levels, the strongest positive relationships between discharge and width were found for runs and where standing water was included (Table 6.1). Reduction in flow from 36% to around 85-86% intensified the width-Q relationships for runs (to a maximum R^2 of 0.67). Although positive relationships were also found for two of the experimental sites for riffle transects, Riviersonderend riffles showed no flow-related trend (Table 6.1), for reasons outlined above. For runs in particular, the best-fit relationships of all were obtained when flow impacted cross-sections (with the inclusion of standing water) were treated separately from those reflecting natural flow conditions, a result probably attributable to the effects of differences in the physical heterogeneity of individual runs within each reach. Coefficients of determination increased from the figures presented in Table 6.1, attaining 0.64 for the Molenaars, 0.65 for the Riviersonderend, and 0.98 for the Du Toits impact locations.

6.3.2 Changes in wetted perimeter and lateral habitat connectivity at low flows

Standardisation of wetted perimeter (WP) and discharge data by recorded maxima for all sites and cross-section types enabled an assessment of the overall effect of flow fluctuations on this key hydraulic parameter. Figure 6.3 depicts the dependency of WP on discharge (R^2 = 0.67), with a clearly accelerating, downward trend in WP with flow reduction (power relationship). For these small streams, the greatest relative decline in WP occurred below approx. 75% of maximum, with values below 50% indicating major habitat loss. Based on observations from the impact phase at the experimental sites, compared with corresponding control data, flow reduction below natural levels (especially in the case of the Riviersonderend reach) resulted in a marked loss of wetted perimeter, and hence, potential invertebrate habitat. Wetted perimeters ranged overall between 20.0 m, for a riffle under the highest discharge recorded, for the Molenaars reach, to only 3.7 m under the most extreme low flow, at the Riviersonderend site. This variation represented an among-site difference in WP of 81%.

The results of independent analysis of overall changes for wetted perimeters in riffles and runs with discharge are illustrated in Figures 6.4 and 6.5, respectively. Riffle WP showed a strongly linear, positive relationship with discharge (Figure 6.4; R^2 = 0.61). A maximum riffle WP of 20.0 m was recorded (Molenaars) and a minimum of 4.6 m (Du Toits). Greatest loss of wetted perimeter occurred over the range of unnaturally low flows. For run transects, the relationship between WP and discharge was even stronger (R^2 = 0.80), with a distinct, non-linear decline in WP with 86% flow reduction, to only 30-40% of maximum WP over the study duration (Figure 6.5). The extremely low WP figures recorded for the Riviersonderend impacted run were the primary drivers of this trend. The wetted perimeter of run cross-sections ranged from only 3.7 m at the Riviersonderend site to 15.8 m at the Molenaars site. Although a distinct threshold was not evident, once flows fell below 10% of maximum there was a 50% or more reduction in habitat as wetted perimeter.

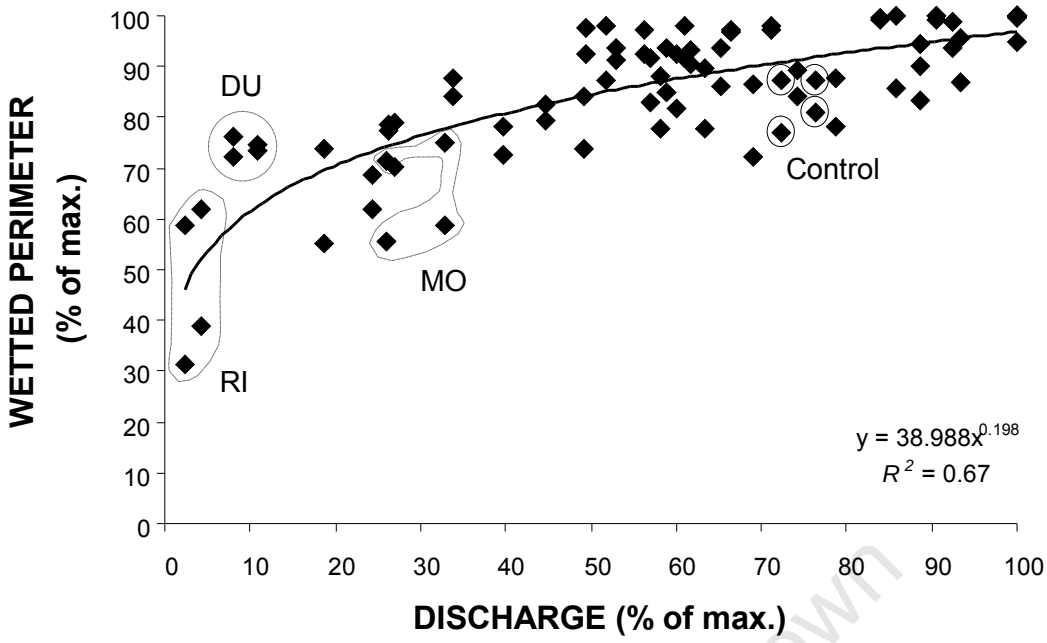


Figure 6.3 **Overall relationship between wetted perimeter and discharge under low flow conditions.** Data collected at unnaturally low flows at experimental sites during the impact phase are delineated by dashed polygons, while corresponding control data (Elands site) are within open circles.

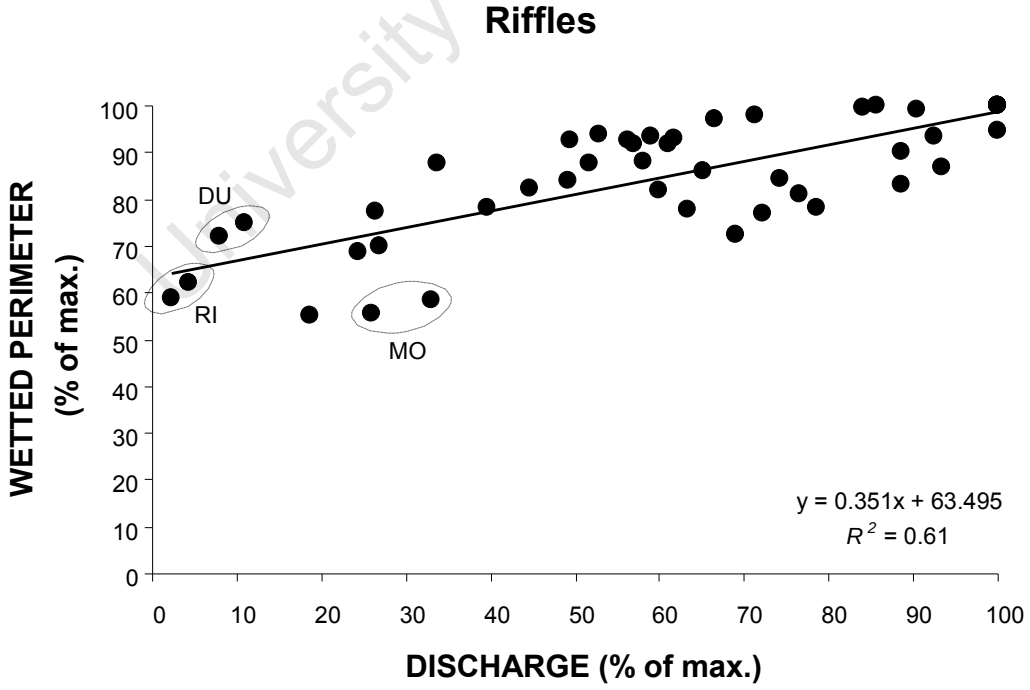


Figure 6.4 **Relationship between riffle wetted perimeter and discharge.** Data collected at unnaturally low flows at experimental sites are delineated by dashed ellipses.

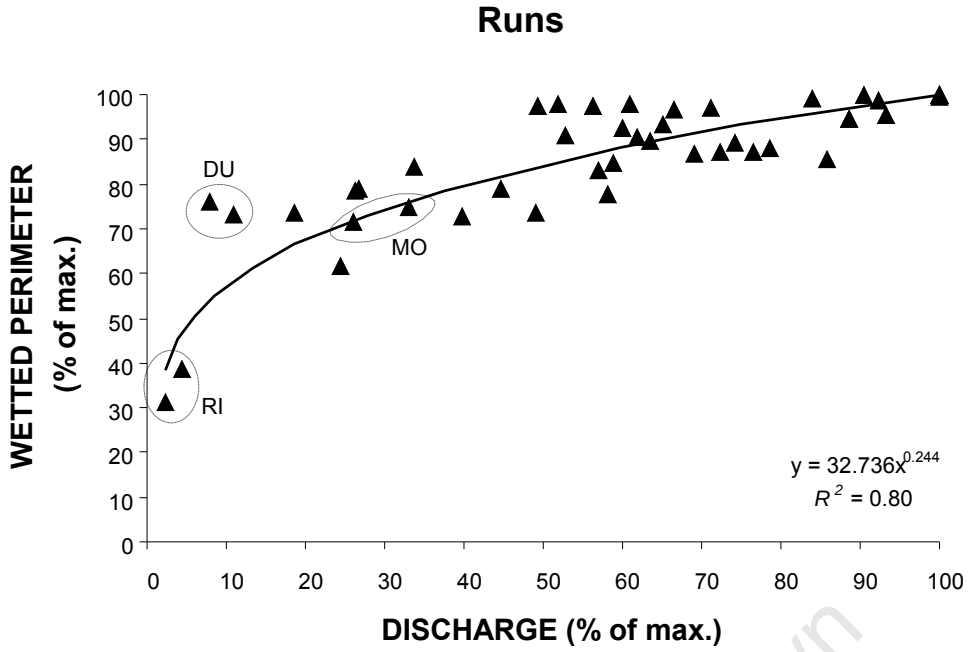


Figure 6.5 Relationship between run wetted perimeter and discharge. Data collected at unnaturally low flows at experimental sites are delineated by dashed ellipses.

To fully understand the effects of natural and unnatural low flows on the wetted perimeters of riffle and run transect biotopes of specific river sites, as well as related impacts on cross-channel habitat connectivity, WP-Q relationships were explored for individual cross-sections in site control and impact locations. The results are presented in Figures 6.6a-d for riffles, and Figures 6.7a-d for runs. The extent to which the river channel at a cross-section was dissected into a series of smaller 'micro-channels' (i.e. widths of flowing or non-flowing water, separated by exposed bed material within the main channel) with flow reduction is shown in the same figures. Analysis of WP-Q relationships for pooled riffle and pooled run data per site showed similar or poorer relationships than those illustrated.

A decrease in wetted perimeter with a decrease in discharge was apparent in all cases, for both riffles and runs (R^2 = 0.49 – 0.99). Both riffle cross-sections at the Elands site showed similarly low natural variability in wetted perimeter (Figure 6.6a). At lowest flows (Feb-Mar) riffle WP decreased to 72% and 81% of maximum, with the former figure just within the range of WP values recorded at extreme low flows (see below). For the more dissimilar runs (Figure 6.7a) WP declines were less than for riffles, with 87% of maximum WP remaining at lowest flow, and ranges were narrow over the study period. Changes in riffle and run lateral connectivity were limited, with a loss of at most two flowing channels at lowest flows (Figures 6.6a and 6.7a, respectively).

Of the experimental sites, the Molenaars displayed the weakest, positive natural WP-Q relationship (riffle - R^2 = 0.49; Figure 6.6b). There was also negligible evidence of increased bed exposure at naturally lowest discharge. In contrast, with further artificial reduction in flow, a pronounced decline in riffle WP was

observed (R^2 = 0.89), with an associated increase in channel dissection (from seven to ten micro-channels; Figure 6.6b). Some 8.9 m of riffle WP were lost at extreme low flows, approaching a halving of WP, as compared with at most 1.6 m naturally (Figure 6.6b). For runs at this site better fit WP-Q relationships were found under natural and unnatural low flows than for riffles (R^2 = 0.78 and 0.97, respectively; Figure 6.7b). Natural low flows resulted in a 22% decrease in run WP, to 8.7 m from the 11.2 m maximum recorded, with little loss of channel connectivity. Marginally greater losses in WP were experienced at extreme low flows (though with an accelerating downward trend evident), with 71-75% of habitat remaining mid-dry season, while channel dissection appeared highest at moderately reduced discharge (Figure 6.7b).

Very strong relationships between WP and discharge (R^2 = 0.85-0.99) were recorded for all of the narrow cross-sections at the Du Toits site (Figures 6.6c and 6.7c). Despite a natural halving of discharge from maximum over the study's duration in February, a relatively high percentage of riffle habitat (92%) remained as wetted perimeter, with a loss from maximum of 0.7 m, and the number of channels remained constant (Figure 6.6c). With manipulated reduction in discharge to levels far below those recorded historically (Chapter 4), WP decreased, as a power function of discharge (R^2 = 0.99), to 72% of maximum. Parallel with the decrease was a clear increase in riffle exposure, with a shift from a single wetted channel to three separate narrower ones (Figure 6.6c). Although under natural conditions at the Du Toits site, the change in run WP was extremely limited over the dry season, remaining around 97% of maximum in February, there remained a well developed relationship between this variable and discharge (R^2 = 0.86; Figure 6.7c). In contrast with this negligible 3% difference, extreme low flows induced a 27% loss in run WP, representing 1.9 m of actual perimeter. Furthermore, comparison of control and impact runs showed a distinct loss of connectivity with flow reduction in the latter case (Figure 6.7c).

Similarly strong relationships between riffle and run WP and discharge (R^2 = 0.84-0.99) were recorded for the other site at which an extreme reduction in flow took place, the Riviersonderend (Figures 6.6d and 6.7d). A naturally marked midsummer discharge decline (to only 19% of the maximum recorded) resulted in a near-halving of riffle WP from maximum, with the loss of 4 m of habitat (Figure 6.6d). As shown for wetted width above, the impacted riffle cross-section was less responsive to large-scale flow reduction than the control, although a 41% loss in WP (3.6 m) was recorded from maximum. No changes in riffle connectivity were discernible at either natural or unnatural flow minima (Figure 6.6d). For both control and impact runs, strongly non-linear decreases in WP occurred as flow decreased to dry season minima (Figure 6.7d). The natural decline of 26% from maximum was well below the 45% recorded for a riffle at the same location, and occurred in concert with a clear loss of connectivity (an increase from two to four micro-channels). The greatest decrease in WP, observed for the flow-impacted run, far exceeded that occurring at natural low flows, reaching 69% at the most extreme flow (Figure 6.7d). This represented only 3.7 m of remaining WP as habitat (of a maximum of 11.9 m) and was coincident with a decrease in the channel number by one (through drying). Some 25% more WP remained in the impacted riffle than the run at such flows.

6.3.3 Low flow effects on the hydraulic character of riffle and run cross-sections: depth and velocity as indicators

Summary statistics indicating site-specific changes in depth and velocity of riffles and runs with fluctuations in natural and unnatural low flows (based on the profiles depicted in Appendix 6.1) are presented in Tables 6.2 and 6.3.

Comparison of hydraulics for riffle and run transect biotopes

Comparison of summary statistics for riffle and run transect biotopes (Tables 6.2 and 6.3; see Section 3.4.1. for terms) showed firstly that trends in hydraulic character were sustained within and among river reaches, irrespective of the natural differences in local geomorphology highlighted by depth and velocity distribution profiles (Appendix 6.1). Comparison of riffle and run cross-section pairs within the control (Elands) site provided evidence that some within-reach hydraulic heterogeneity could be expected at low flows. The Du Toits site exhibited fairly simple, homogenous run and riffle profiles, while hydraulic differences between riffle and run transects were least pronounced for the Riviersonderend mountain-stream reach, where both biotopes were similarly heterogeneous.

Hydraulically, as expected, riffles were consistently shallower and faster flowing than runs within the same reach over the natural low flow range. Furthermore, across all sites, lower minima, maxima, and average depths were recorded for riffles than for runs. In contrast, riffles exhibited far higher velocities than runs, as well as a wider range of values. Comparison of the means and ranges of near-bottom velocities (NBV) with mean column velocities (0.6V) for riffles and runs showed that, in the vast majority of cases, NBV values were lower (Tables 6.2 and 6.3), as expected with increased frictional resistance close to the bed (Gordon *et al.* 1992). The few cases (four) where NBV exceeded 0.6V were for riffles, suggesting an influence of turbulence on the velocity profile (Carling 1992; Hart *et al.* 1996; Robson *et al*. 1999).

Riffles generally exhibited more variable depth and velocity distributions than runs, due to the naturally higher bed roughness associated with the protrusion of large substratum elements relative to depth, and prevalence of chaotic flows (Davis and Barmuta 1989; Bouckaert and Davis 1998; Appendix 6.1). There were fewer deep sections, especially wide ones, and velocities increased or decreased across the channel more sharply than across runs. Also, there was a less consistent relationship between depth and velocity, than for runs. This was most likely due to the dissipative nature of turbulent flow and inherited turbulence from flow separation occurring upstream due to upstream roughness elements (Hart *et al.* 1996; Robson *et al*. 1999), as well as differences in hydraulic geometry.

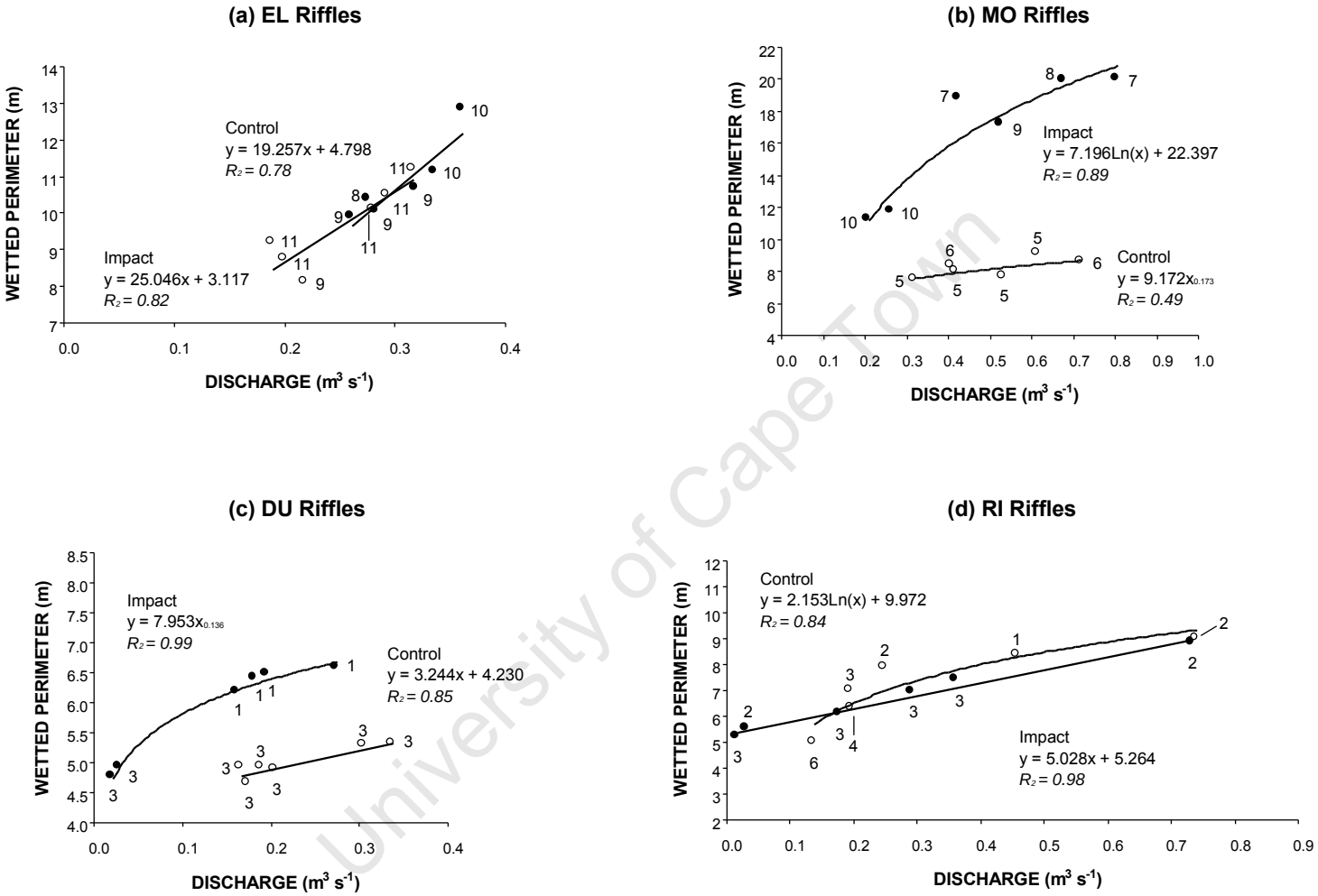


Figure 6.6 **Best-fit relationships between wetted perimeter (m) and discharge (m^3 s^{-1}) for riffles at the (a) Elands, (b) Molenaars, (c) Du Toits and (d) Riviersonderend sites.** Control - open circles. Impact - solid circles. Numbers at individual data points represent the number of 'micro-channels' at the observed discharge. Note the different scales among plots.

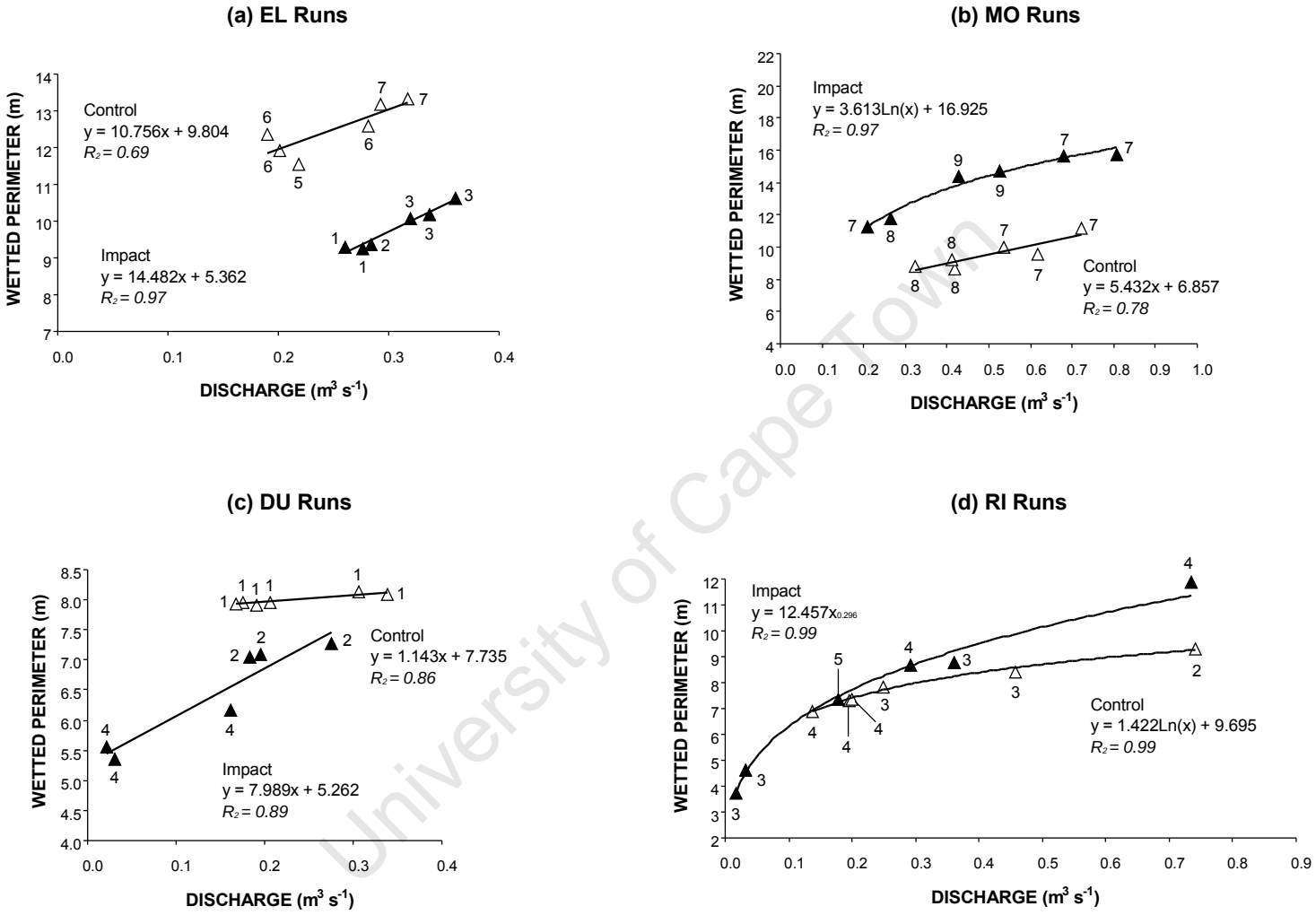


Figure 6.7 **Best-fit relationships between wetted perimeter (m) and discharge (m^3 s^{-1}) for runs at the (a) Elands, (b) Molenaars, (c) Du Toits and (d) Riviersonderend sites.** Control - open triangles. Impact - solid triangles. Numbers at individual data points represent the number of 'micro-channels' at the observed discharge. Note the different scales among plots.

Table 6.2 **Summary statistics indicating site-specific changes in riffle hydraulic character (depth and velocity) during the study and in relation to natural and experimental discharge fluctuations.** Site control and impact locations were treated individually. Depth (m); 0.6V – mean column velocity (m s^{-1}); NBV – near-bed velocity (m s^{-1}); Q_{inst} – instantaneous discharge (m^3 s^{-1}); %ile - flow percentile, derived from the corresponding monthly FDC for each site; *n* – number of in-water points; SD – standard deviation from mean.

SITE MONTH	CONTROL RIFFLE									IMPACT RIFFLE								
				Depth (m)		0.6V		NBV					Depth (m)		0.6V		NBV	
	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
EL																		
Dec	0.317	95	17	0.020 - 0.330	0.171 (0.098)	0.055 - 0.578	0.239 (0.152)	0.048 - 0.452	0.178 (0.107)	0.361	87	19	0.020 - 0.330	0.182 (0.089)	0 - 0.670	0.256 (0.215)	0 - 0.564	0.224 (0.161)
Jan	0.281	86	18 - 20	0.010 - 0.330	0.128 (0.106)	0 - 0.392	0.129 (0.114)	0 - 0.432	0.120 (0.116)	0.320	68	21	0.005 - 0.350	0.127 (0.100)	0 - 0.902	0.311 (0.258)	0 - 0.713	0.261 (0.217)
Feb	0.219	93	23	0.010 - 0.280	0.131 (0.079)	0 - 0.558	0.183 (0.137)	0.001 - 0.558	0.194 (0.155)	0.276	69	22	0.003 - 0.280	0.117 (0.075)	0 - 0.644	0.256 (0.205)	0 - 0.644	0.238 (0.196)
Mar	0.201	96	27	0.020 - 0.470	0.160 (0.102)	0.028 - 0.591	0.239 (0.163)	0 - 0.558	0.207 (0.154)	0.261	71	23	0.020 - 0.270	0.142 (0.065)	0 - 0.690	0.261 (0.187)	0 - 0.677	0.231 (0.181)
Apr	0.190	96	28 - 29	0.001 - 0.320	0.156 (0.087)	0.001 - 0.578	0.210 (0.176)	0.001 - 0.505	0.171 (0.128)	0.284	75	25	0.010 - 0.250	0.134 (0.074)	0 - 0.892	0.254 (0.227)	0 - 0.892	0.202 (0.197)
May	0.293	95	26 - 27	0.040 - 0.340	0.178 (0.096)	0.001 - 0.832	0.234 (0.213)	0.001 - 0.832	0.208 (0.196)	0.337	93	23 - 24	0.002 - 0.315	0.177 (0.081)	0 - 0.902	0.317 (0.287)	0 - 0.793	0.265 (0.208)
MO																		
Dec	0.721	72	13	0.020 - 0.430	0.182 (0.124)	0.048 - 1.190	0.428 (0.362)	0.055 - 1.408	0.406 (0.384)	0.808	59	15	0.020 - 0.320	0.158 (0.086)	0 - 1.805	0.464 (0.505)	0 - 1.170	0.388 (0.317)
Jan	0.535	74	15	0.010 - 0.440	0.142 (0.128)	0 - 1.054	0.396 (0.320)	0 - 1.014	0.375 (0.315)	0.527	76	21	0.005 - 0.300	0.123 (0.096)	0 - 1.537	0.266 (0.319)	0 - 0.987	0.250 (0.217)
Feb	0.322	96	20	0.003 - 0.380	0.140 (0.101)	0.061 - 1.107	0.419 (0.292)	0.001 - 1.107	0.395 (0.312)	0.210	99	23	0.003 - 0.370	0.092 (0.097)	0 - 0.902	0.347 (0.267)	0 - 0.856	0.335 (0.262)
Mar	0.419	87	23	0.010 - 0.380	0.146 (0.099)	0.001 - 1.008	0.400 (0.284)	0.001 - 1.134	0.349 (0.296)	0.266	100	27	0.003 - 0.360	0.098 (0.087)	0 - 1.286	0.379 (0.313)	0 - 1.253	0.370 (0.305)
Apr	0.411	88	25	0.005 - 0.390	0.137 (0.102)	0.004 - 1.329	0.351 (0.326)	0.001 - 1.428	0.289 (0.334)	0.427	86	32 - 33	0.020 - 0.430	0.131 (0.110)	0.108 - 1.269	0.421 (0.251)	0.028 - 1.091	0.383 (0.260)
May	0.618	84	26	0.005 - 0.410	0.161 (0.118)	0.001 - 1.215	0.370 (0.325)	0.001 - 1.071	0.336 (0.295)	0.679	82	27 - 28	0.020 - 0.440	0.160 (0.103)	0.058 - 0.971	0.450 (0.290)	0.058 - 1.060	0.414 (0.322)

Table 6.2 Continued.

SITE MONTH	CONTROL RIFFLE									IMPACT RIFFLE								
				Depth (m)		0.6V		NBV					Depth (m)		0.6V		NBV	
	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
DU																		
Dec	0.338	29	15	0.020 - 0.240	0.100 (0.064)	0.048 - 0.909	0.353 (0.301)	0.048 - 0.948	0.340 (0.305)	0.196	86	13	0.060 - 0.340	0.158 (0.071)	0.108 - 0.717	0.347 (0.162)	0.108 - 0.482	0.266 (0.112)
Jan	0.175	67	15	0.005 - 0.200	0.095 (0.057)	0.055 - 1.285	0.475 (0.379)	0.055 - 1.285	0.470 (0.370)	0.183	60	13	0.040 - 0.190	0.113 (0.043)	0 - 0.862	0.346 (0.244)	0 - 0.631	0.290 (0.173)
Feb	0.167	56	13	0.020 - 0.200	0.098 (0.052)	0 - 1.110	0.440 (0.307)	0 - 1.056	0.417 (0.311)	0.022	100	17	0.005 - 0.190	0.053 (0.048)	0 - 0.406	0.150 (0.121)	0 - 0.406	0.149 (0.121)
Mar	0.190	32	15	0.020 - 0.170	0.097 (0.046)	0.035 - 1.438	0.557 (0.396)	0.035 - 1.438	0.525 (0.411)	0.030	100	17	0.010 - 0.200	0.057 (0.044)	0 - 0.326	0.164 (0.097)	0 - 0.432	0.166 (0.108)
Apr	0.206	52	17	0.020 - 0.190	0.082 (0.054)	0.035 - 1.471	0.508 (0.398)	0.035 - 1.345	0.484 (0.409)	0.162	69	33	0.002 - 0.260	0.085 (0.067)	0 - 0.564	0.239 (0.158)	0 - 0.452	0.200 (0.121)
May	0.306	71	20	0.030 - 0.250	0.116 (0.067)	0 - 1.349	0.520 (0.383)	0 - 1.339	0.384 (0.364)	0.275	75	20	0.025 - 0.340	0.156 (0.076	0 - 0.554	0.271 (0.188)	0 - 0.406	0.177 (0.119)
RI																		
Dec	0.195	70	12	0.020 - 0.210	0.107 (0.066)	0 - 1.299	0.470 (0.467)	0 - 1.220	0.407 (0.407)	0.179	79	15	0.030 - 0.330	0.147 (0.085)	0.101 - 1.438	0.373 (0.383)	0.095 - 1.061	0.337 (0.304)
Jan	0.250	32	16	0.005 - 0.240	0.121 (0.083)	0 - 1.087	0.392 (0.354)	0 - 1.087	0.391 (0.337)	0.292	26	17	0.005 - 0.380	0.157 (0.096)	0 - 0.882	0.409 (0.273)	0 - 0.882	0.392 (0.285)
Feb	0.138	68	12 - 13	0.005 - 0.200	0.071 (0.068)	0 - 0.604	0.302 (0.189)	0 - 0.644	0.314 (0.188)	0.017	100	13 - 15	0.020 - 0.230	0.088 (0.058)	0 - 1.001	0.249 (0.314)	0 - 0.770	0.227 (0.275)
Mar	0.199	50	18 - 19	0.010 - 0.240	0.093 (0.081)	0 - 0.763	0.301 (0.221)	0 - 0.763	0.308 (0.213)	0.032	100	17	0.001 - 0.200	0.096 (0.055)	0.015 - 1.173	0.247 (0.266)	0.042 - 1.147	0.239 (0.262)
Apr	0.458	47	28 - 32	0.020 - 0.310	0.113 (0.074)	0 - 1.435	0.521 (0.437)	0 - 1.376	0.473 (0.379)	0.361	54	25	0.030 - 0.340	0.178 (0.102)	0.001 - 1.259	0.500 (0.376)	0 - 1.021	0.401 (0.319)
May	0.741	53	16 - 17	0.050 - 0.450	0.196 (0.121)	0.001 - 2.986	0.702 (0.764)	0.001 - 1.310	0.539 (0.437)	0.735	53	20	0.060 - 0.450	0.271 (0.119)	0.050 - 1.530	0.542 (0.333)	0.050 - 1.045	0.475 (0.269)

Table 6.3 **Summary statistics indicating site-specific changes in run hydraulic character (depth and velocity) during the study and in relation to natural and experimental discharge fluctuations.** Site control and impact locations were treated individually. Depth (m); 0.6V – mean column velocity (m s^{-1}); NBV – near-bed velocity (m s^{-1}); Q_{inst} – instantaneous discharge (m^3 s^{-1}); %ile - flow percentile, derived from the corresponding monthly FDC for each site; *n* – number of in-water points; SD – standard deviation from mean.

SITE MONTH	CONTROL RUN									IMPACT RUN								
				Depth (m)		0.6V		NBV					Depth (m)		0.6V		NBV	
	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
EL																		
Dec	0.317	95	16	0.140 - 0.440	0.325 (0.103)	0.028 - 0.200	0.103 (0.054)	0.028 - 0.214	0.077 (0.052)	0.361	87	15	0.020 - 0.480	0.273 (0.127)	0.004 - 0.192	0.104 (0.060)	0 - 0.121	0.063 (0.040)
Jan	0.281	86	20	0.005 - 0.460	0.228 (0.118)	0.025 - 0.200	0.114 (0.051)	0 - 0.194	0.098 (0.056)	0.320	68	16	0.010 - 0.460	0.249 (0.122)	0 - 0.207	0.100 (0.081)	0 - 0.187	0.066 (0.063)
Feb	0.219	93	22	0.040 - 0.410	0.219 (0.108)	0.004 - 0.273	0.106 (0.063)	0.001 - 0.273	0.096 (0.076)	0.276	69	17	0.030 - 0.470	0.238 (0.128)	0 - 0.167	0.088 (0.060)	0 - 0.148	0.054 (0.054)
Mar	0.201	96	23	0.080 - 0.390	0.189 (0.090)	0 - 0.273	0.099 (0.074)	0 - 0.181	0.083 (0.064)	0.261	71	18	0.005 - 0.430	0.235 (0.122)	0 - 0.200	0.101 (0.055)	0.001 - 0.174	0.080 (0.055)
Apr	0.190	96	23	0.050 - 0.420	0.190 (0.094)	0.015 - 0.267	0.107 (0.069)	0 - 0.240	0.084 (0.069)	0.284	75	16	0.020 - 0.430	0.259 (0.100)	0.028 - 0.177	0.102 (0.045)	0.001 - 0.157	0.065 (0.047)
May	0.293	95	17	0.050 - 0.470	0.245 (0.117)	0.028 - 0.336	0.130 (0.090)	0 - 0.336	0.106 (0.091)	0.337	93	18	0.020 - 0.570	0.286 (0.148)	0.001 - 0.197	0.090 (0.068)	0.001 - 0.197	0.053 (0.059)
MO																		
Dec	0.721	72	16	0.020 - 0.580	0.233 (0.157)	0 - 0.505	0.287 (0.143)	0 - 0.419	0.236 (0.132)	0.808	59	16	0.010 - 0.320	0.179 (0.092)	0 - 0.611	0.282 (0.209)	0 - 0.631	0.209 (0.181)
Jan	0.535	74	16	0.020 - 0.550	0.212 (0.148)	0 - 0.425	0.197 (0.140)	0 - 0.346	0.174 (0.110)	0.527	76	24	0.010 - 0.320	0.158 (0.088)	0.028 - 0.492	0.222 (0.118)	0 - 0.406	0.178 (0.107)
Feb	0.322	96	19	0.010 - 0.530	0.207 (0.143)	0 - 0.339	0.171 (0.112)	0 - 0.326	0.143 (0.106)	0.210	99	25	0.020 - 0.210	0.098 (0.059)	0 - 0.505	0.201 (0.139)	0 - 0.459	0.191 (0.130)
Mar	0.419	87	18	0.060 - 0.570	0.247 (0.140)	0.001 - 0.359	0.205 (0.113)	0.001 - 0.306	0.172 (0.099)	0.266	100	25	0.020 - 0.220	0.121 (0.065)	0 - 0.545	0.209 (0.143)	0 - 0.511	0.189 (0.131)
Apr	0.411	88	20	0.020 - 0.540	0.219 (0.153)	0 - 0.538	0.188 (0.148)	0 - 0.538	0.165 (0.148)	0.427	86	26	0.060 - 0.290	0.162 (0.069)	0.001 - 0.545	0.237 (0.160)	0 - 0.584	0.190 (0.158)
May	0.618	84	17	0.050 - 0.630	0.276 (0.164)	0 - 0.515	0.245 (0.147)	0 - 0.425	0.184 (0.129)	0.679	82	25	0.050 - 0.320	0.176 (0.071)	0.001 - 1.190	0.349 (0.263)	0 - 1.031	0.262 (0.233)

Table 6.3 Continued.

SITE MONTH	CONTROL RUN									IMPACT RUN								
				Depth (m)		0.6V		NBV					Depth (m)		0.6V		NBV	
	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Q_{inst}	%ile	*n*	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
DU																		
Dec	0.338	29	16	0.060 - 0.176 *0.400	(0.087)	0 - 0.209 0.670	(0.180)	0 - 0.183 0.736	(0.192)	0.196	86	13	0.050 - 0.210	0.153 (0.046)	0 - 0.492	0.210 (0.146)	0 - 0.492	0.200 (0.132)
Jan	0.175	67	16	0.010 - 0.123 0.270	(0.080)	0 - 0.161 0.485	(0.151)	0 - 0.121 0.286	(0.114)	0.183	60	14	0.020 - 0.200	0.125 (0.055)	0 - 0.551	0.225 (0.158)	0 - 0.511	0.190 (0.134)
Feb	0.167	56	17	0.003 - 0.121 0.260	(0.091)	0 - 0.215 0.690	(0.190)	0 - 0.195 0.511	(0.171)	0.022	100	11	0.020 - 0.150	0.055 (0.034)	0 - 0.313	0.123 (0.119)	0 - 0.313	0.121 (0.122)
Mar	0.190	32	17	0.005 - 0.128 0.250	(0.078)	0 - 0.207 0.690	(0.200)	0 - 0.170 0.412	(0.167)	0.030	100	14	0.002 - 0.100	0.054 (0.028)	0 - 0.353	0.113 (0.118)	0 - 0.353	0.094 (0.099)
Apr	0.206	52	14	0.025 - 0.137 0.250	(0.080)	0 - 0.197 0.664	(0.181)	0 - 0.158 0.624	(0.179)	0.162	69	19	0.020 - 0.180	0.096 (0.052)	0 - 0.525	0.204 (0.164)	0 - 0.392	0.164 (0.120)
May	0.306	71	16	0.010 - 0.170 0.320	(0.096)	0.001 - 0.245 0.743	(0.208)	0 - 0.209 0.574	(0.191)	0.275	75	18	0.040 - 0.230	0.135 (0.072)	0.001 - 0.515	0.225 (0.175)	0.001 - 0.455	0.198 (0.148)
RI																		
Dec	0.195	70	14	0.040 - 0.185 0.300	(0.087)	0 - 0.156 0.372	(0.105)	0 - 0.148 0.379	(0.107)	0.179	79	14	0.050 - 0.520	0.256 (0.153)	0 - 0.326	0.111 (0.096)	0 - 0.267	0.083 (0.091)
Jan	0.250	32	17	0.005 - 0.174 0.340	(0.097)	0 - 0.184 0.942	(0.243)	0 - 0.123 0.419	(0.138)	0.292	26	19	0.010 - 0.580	0.235 (0.180)	0 - 0.346	0.174 (0.105)	0 - 0.353	0.139 (0.097)
Feb	0.138	68	16 - 17	0.010 - 0.169 0.320	(0.092)	0 - 0.153 0.445	(0.131)	0 - 0.147 0.363	(0.111)	0.017	100	11	0.030 - 0.310	0.101 (0.091)	0 - 0.081	0.029 (0.030)	0 - 0.081	0.022 (0.030)
Mar	0.199	50	15 - 16	0.030 - 0.191 0.340	(0.089)	0 - 0.186 0.432	(0.158)	0 - 0.122 0.366	(0.137)	0.032	100	25	0.005 - 0.420	0.097 (0.114)	0 - 0.267	0.040 (0.070)	0 - 0.267	0.032 (0.067)
Apr	0.458	47	21 - 22	0.020 - 0.200 0.400	(0.117)	0 - 0.297 1.006	(0.274)	0 - 0.223 0.657	(0.206)	0.361	54	31	0.040 - 0.580	0.232 (0.130)	0 - 0.374	0.186 (0.124)	0 - 0.346	0.149 (0.111)
May	0.741	53	17 - 18	0.090 - 0.296 0.460	(0.129)	0.028 - 0.382 0.847	(0.276)	0 - 0.305 0.777	(0.251)	0.735	53	25	0.020 - 0.580	0.287 (0.145)	0 - 0.516	0.250 (0.177)	0 - 0.471	0.204 (0.158)

* The figure for maximum depth for DU of 0.400 m is an outlier. If excluded, mean depth would be at a more realistic value of 0.161, with an associated reduction in SD to 0.065.

Riffle depths and velocities naturally decreased with a decrease in flow across all sites and locations (discussed further below), but at natural low flows narrow, fairly deep sections of channel and occasional high-velocity peaks remained. As with runs, substantial depth and velocity increases required relatively high increases in discharge. Lateral shifts in areas of peak velocity, and particularly, greatest depth, occurred infrequently and mostly also as a result of a major change in discharge (Appendix 6.1). In runs, more so than in riffles, although there was a natural increase in the width of channel exposed at lower flows dissection of the wetted profile into micro-channels was fairly low, with wide sections of deep water and a broad velocity range generally intact.

Riffle depths and velocities at low flows

Among all sites, riffles were shallowest for the Riviersonderend site, with a (minimum) average depth under naturally lowest flow conditions of 0.071 m (February). At the same time of year, the average (minimum) depth of the deepest riffle, at the Molenaars site, was effectively double, at 0.137 m. Maximum average depths ranged from 0.116 m, for the Du Toits reach in May, to 0.196 m for the Riviersonderend River with the onset of early autumn higher flows. Over the entire study, the greatest depth recorded across riffle sections, 0.470 m, was recorded for the Elands midsummer. Lowest and highest average (0.6V) riffle velocities recorded under natural low flow regimes were 0.129 m s^{-1} for the Elands reach and 0.702 m s^{-1} (reflecting elevated autumn flows) in the Riviersonderend River, respectively. Overall, the lowest and highest maximum velocities recorded in a riffle at natural low flows were 0.392 m s^{-1} (Elands) and 2.986 m s^{-1} (Riviersonderend, in May). Near-bed riffle velocities showed highly similar flow-related responses to those of 0.6V velocities. Cells of zero velocity were occasionally recorded along riffle sections (Table 6.2 and Appendix 6.1).

Assessed changes in riffle average depths and velocities under exceptionally low flows (Feb-Mar) were based on Table 6.2 statistics. Accepting natural hydraulic variation between riffle cross-sections within a reach, and that greater natural differences in mean depth or velocity may have been experienced at a site in months other than those of the impact phase, direct comparison of control and impact figures for the impact months was used as one means of establishing hydraulic response to extreme low flows. A second approach, that circumvented the possible influence of natural differences in hydraulic character of control and impact riffles, was to compare mean hydraulic conditions in the preceding month, January, for the same impacted cross-section, with impact data. This assessment (see Table 6.4), which was similarly performed for runs below, indicated sometimes pronounced effects of extreme low flows on riffle depth and velocity.

Results obtained for the Elands site, based on analysis (a), showed that the natural change in hydraulic conditions in riffles during a dry season could be as high as 40% (Table 6.4). Moreover, both analyses demonstrated that even the direction of response could vary depending on differences in riffle architecture (and possibly also experimental error in discharge measurement).

Table 6.4 **Percentage and direction of response (increase ↑, decrease ↓) in riffle average depths and average velocities (0.6V) at extreme low flows, when compared with (a) natural flow conditions in the corresponding control location, and (b) conditions in January for the same impacted cross-section.** Relative differences recorded under natural low flows at the control site are provided for comparison.

SITE (flow reduction)	(a) CONTROL VERSUS IMPACT RIFFLE		(b) JAN COMPARED WITH IMPACT MONTH	
	Feb % change	Mar % change	Feb Control vs. Impact % change	Mar Control vs. Impact % change
EL (Control - 0% ↓ Q)				
Depth	10.7 ↓	11.3 ↓	2.3 ↑ vs. 7.9 ↓	25.0 ↑ vs. 11.8 ↑
0.6V	39.9 ↑	9.2 ↑	41.9 ↑ vs. 17.7 ↓	85.3 ↑ vs. 16.1 ↓
MO (34.8 & 36.5% ↓ Q)				
Depth	34.3 ↓	32.9 ↓	1.4 ↓ vs. 25.2 ↓	2.8 ↑ vs. 20.3 ↓
0.6V	17.2 ↓	5.3 ↓	5.8 ↑ vs. 30.5 ↑	1.0 ↑ vs. 42.5 ↑
DU (86.8 & 84.2% ↓ Q)				
Depth	45.9 ↓	41.2 ↓	3.2 ↑ vs. 53.1 ↓	2.1 ↑ vs. 49.6 ↓
0.6V	65.9 ↓	70.6 ↓	7.4 ↓ vs. 56.6 ↓	17.3 ↑ vs. 52.6 ↓
RI (87.7 & 83.9% ↓ Q)				
Depth	23.9 ↑	3.2 ↑	41.3 ↓ vs. 43.9 ↓	23.1 ↓ vs. 38.9 ↓
0.6V	17.5 ↓	17.9 ↓	23.0 ↓ vs. 39.1 ↓	23.2 ↓ vs. 39.6 ↓

Reduction in discharge to just below historical minima in the Molenaars River resulted in a decrease in average riffle depth of *c.* 20-34%, to 0.09 m (cf. a minimum mean depth of 0.14 m under natural flows; Tables 6.2 and 6.4). There was loss of the widest section of moderately deep riffle, with flowing-channel dissection. Moreover, although there were still two channels deeper than 0.25 m in early March, they were narrow (Appendix 6.1). Despite average velocity being 17% lower, at 0.347 m s^{-1}, for the impacted riffle than the natural dry-season mean (0.419 m s^{-1} in Feb), closer examination of the data (analysis (b), Tables 6.2 and 6.4) showed that mean values actually increased at extremely low discharges. There was a decline in maximum riffle velocity, however, especially in February, as well as a decrease in the highest velocities in each of the subsidiary channels (Appendix 6.1).

The most distinct discharge-hydraulics response of all sites was found for the Du Toits site (Table 6.4). Reduction in dry season flow to far below absolute historical minima (Chapter 4) resulted in an approximate halving of riffle mean depth, on the basis of all analyses, to 0.053 m (control riffle depth = 0.098 m; Table 6.2). The second-most deep channel section was lost, and the remaining moderately deep section narrowed (Appendix 6.1). The conclusive decrease in mean velocity was even more dramatic, in the order of 53-71% (Table 6.4); changes in natural means were slight over the same period. In February, at 0.150 m s^{-1}, it was 66% lower than the control average of 0.440 m s^{-1} (Table 6.2). There was also a decrease in maximum

velocity to only 0.406 m s^{-1}, the lowest overall. These changes were coupled with a dramatic increase in riffle width experiencing zero flow (Appendix 6.1 and below).

Although, at first there appeared to be an increase in mean depth for the flow-impacted riffle at the Riviersonderend site (0.088 m cf. 0.071 m for the control), as mentioned previously the riffle was atypical, and differed especially in depth compared to the control riffle (Table 6.2 and Appendix 6.1). However, analysis (b) demonstrated that the control and, more so, the impacted riffle showed decreases in mean depth from January to peak dry season (Table 6.4). Although there was still a wide area of fairly deep water (maximum depth = 0.23 m), much of the latter riffle was flowing slowly, with an average velocity of 0.249 m s^{-1} (cf. control riffle 0.6V = 0.302 m s^{-1}; Table 6.2). Indeed, both analyses identified a clear decrease in mean velocity (17-40%), and to a greater extent than that experienced naturally midsummer (Table 6.4). Maximum velocity remained high with major flow reduction, at 1.001 m s^{-1}, exceeding the natural maximum (0.604 m s^{-1}; Table 6.2), probably due to less water being forced through a narrower, bedrock-controlled section (pers. obs.). There was a marked increase in zero-velocity cells, however, compared with antecedent conditions (see below and Appendix 6.1).

Run depths and velocities at low flows

Comparing runs at all sites over the full range of natural flows examined (Table 6.3 and Appendix 6.1), average run depths ranged from as little as 0.121 m (Du Toits control location, in the lowest flow month, Feb) to 0.325 m (Elands reach, at highest observed discharge, Dec). Overall, the Molenaars reach had the deepest runs ($depth_{max}$ = 0.63 m, in autumn), while the lowest natural $depth_{max}$ of 0.250 m was recorded for the Du Toits site. Over the study duration, at natural low flows, average 0.6V values in runs ranged from 0.088 m s^{-1} to a maximum mean of 0.382 m s^{-1}. During the driest months, natural average velocities ranged from 0.088 m s^{-1} (Elands) to 0.215 m s^{-1} for the Du Toits control run. The highest maximum velocity was recorded for the Riviersonderend, at 1.006 m s^{-1}, during elevated April flow, while the lowest maximum, 0.167 m s^{-1}, occurred midsummer within the Elands reach. In runs, near-bottom velocities showed responses highly similar to those of 0.6V figures. Mean figures ranged from 0.053 (Elands) to 0.305 m s^{-1} (correspondingly to the time of highest mean velocity, in the Riviersonderend River. The range of NBV maxima, 0.121-0.777 m s^{-1}, was recorded for the same sites, respectively. Minimum depths and velocities were again rather meaningless, as run depths in the order of only a few centimetres and zero velocities occurred under both natural and extreme low flows (Table 6.3). However, the proportions of run width of zero velocities and of depths below specified minima were potentially ecologically significant factors (Section 6.7).

A similar assessment to that performed for riffles, on the effects of unnaturally low, dry-season flows on run average depths and velocities (using Table 6.3 statistics), showed that runs were also hydraulically impacted (Table 6.5).

Table 6.5 Percentage and direction of response in run average depths and average velocities (0.6V) at extreme low flows during the impact phase at experimental locations, when compared with: (a) natural flow conditions in the corresponding control location; (b) conditions in January for the same impacted cross-section. Relative differences recorded under natural low flows at the control site are provided for comparative purposes.

SITE (flow reduction)	(a) CONTROL VERSUS IMPACT RUN		(b) JAN COMPARED WITH IMPACT MONTH	
	Feb % change	Mar % change	Feb Control vs. Impact % change	Mar Control vs. Impact % change
EL (Control - 0% ↓ Q)				
Depth	8.7 ↑	24.3 ↑	3.9 ↓ vs. 4.4 ↓	17.1 ↓ vs. 5.6 ↓
0.6V	17.0 ↓	2.0 ↑	7.0 ↓ vs. 12.0 ↓	13.2 ↓ vs. 1.0 ↑
MO (34.8 & 36.5% ↓ Q)				
Depth	52.7 ↓	51.0 ↓	2.4 ↓ vs. 38.0 ↓	16.5 ↑ vs. 23.4 ↓
0.6V	17.5 ↑	2.0 ↑	13.2 ↓ vs. 9.5 ↓	4.1 ↑ vs. 5.9 ↓
DU (86.8 & 84.2% ↓ Q)				
Depth	54.5 ↓	57.8 ↓	1.6 ↓ vs. 56.0 ↓	4.1 ↑ vs. 56.8 ↓
0.6V	42.8 ↓	45.4 ↓	33.5 ↑ vs. 45.3 ↓	28.6 ↑ vs. 49.8 ↓
RI (87.7 & 83.9% ↓ Q)				
Depth	40.2 ↓	49.2 ↓	2.9 ↓ vs. 57.0 ↓	9.8 ↑ vs. 58.7 ↓
0.6V	81.0 ↓	78.5 ↓	16.8 ↓ vs. 83.3 ↓	1.1 ↑ vs. 77.0 ↓

As for riffles, the results obtained for the Elands site for analysis (a) showed its limited use in assessing hydraulic response, as natural intra-reach differences in run hydraulics were entirely responsible for the apparent increase in mean depth (Table 6.5). The second form of analysis (b) was again more reliable in detecting actual response, showing that there was a small, natural decrease in mean depth for both runs evaluated (Tables 6.3 and 6.5).

Flow diversion upstream of the Molenaars impact location resulted in a pronounced reduction in run mean depth relative to recorded natural declines. Associated with the January-February flow decrease, mean depth decreased most, from 0.212 m to 0.207 m in the non-impacted run, and from 0.158 m to 0.098 m for the flow-impacted one. Trends in velocity were less apparent. The higher mean velocity for the impact run (0.201 m s^{-1} - highest of all experimental sites) as compared with the control run (0.171 m s^{-1}), and higher maximum velocity for the former run in February than January, confounded understanding of the river's response to abnormally low flows. On closer scrutiny (Table 6.5 - analysis (b)), however, small decreases in mean velocity for both runs, and two areas of high velocity were lost in the impacted run (Appendix 6.1).

Extreme flow reduction strongly impacted run mean depth and velocity in the Du Toits reach (analyses (a) and (b); Table 6.5), in the former instance particularly because the channel exhibits few naturally deep areas (Appendix 6.1). The flow-impacted run became extremely shallow throughout its profile, with an average depth of around 0.055 m (cf. 0.121 m, a small decrease from Jan for the hydraulically fairly similar control

run), more than a halving of mean depth (55-58%). The majority of run width was below 0.05 m deep, with both major flowing channel sections reduced below 0.10 m in depth (Appendix 6.1). The results for mean 0.6V showed a definite decline from 0.225 m s^{-1} to 0.113 m s^{-1} (*c.* 43-50%) with flow diversion midsummer, in contrast with an increase for both months under a natural low flow regime. This pattern was coupled with a loss of high-velocity areas (Table 6.3 and Appendix 6.1).

The impacted run at the Riviersonderend site showed a pronounced response to flow diversion (Table 6.5). Both analyses indicated a marked decline in mean water depth of around 40-59%, from 0.235 m in January to only 0.097 m in March, though maximum depth remained similar to that of the non-impacted run and was highest of all impacted runs (Table 6.3). Although the cross-sectional morphology of the Riviersonderend's impact run was such that a short section of deeper water remained, the section's velocity was far lower than under natural conditions (Appendix 6.1). Indeed, run 0.6V was extremely low at experimentally reduced discharges, reaching only 0.029 m s^{-1} in February – the lowest of all experimental locations (cf. natural run 0.6V = 0.153 m s^{-1}; Table 6.3). Analyses showed a corresponding reduction in mean velocity in the order of 77-83%, by far the greatest response to extreme low flows observed (Table 6.5). Additionally, the lowest maximum velocity of all impacted runs was recorded for the Riviersonderend at 0.081 m s^{-1} (cf. around 0.320 m s^{-1} at natural peak low flows; Table 6.3). The loss of all high-velocity areas also was apparent, with even the few remaining deep sections barely flowing and the loss of an entire flowing secondary channel.

Generalised relationships between depth, velocity, and discharge

Analysis of relationships between mean depth, mean velocity and discharge magnitude, irrespective of the temporal flow sequence or character of individual cross-sections (Table 6.6), supported the findings outlined above. For among-site comparisons, hydraulic variables were plotted against normalised instantaneous discharge while relationships for individual sites were based on Q_{inst} figures. In all but one case examined (run mean 0.6V at the control site), the relationship between hydraulics and low flows was positive, with a decrease in either average depth or velocity with a decrease in discharge. Weak to moderate positive trends, largely non-linear, were found for pooled data from all sites, as well as for runs and riffles separately (Table 6.6); non-normalised data yielded better fits. The closest fit was between run mean velocity and instantaneous discharge (R^2 = 0.48).

Generally, better fit relationships were obtained when riffles and runs were examined independently, and for individual sites (Table 6.6). However, for the control situation, the only strong trend was for Q-mean depth for run transect biotopes (R^2 = 0.77). For the Molenaars site, the clear relationship between mean depth and extreme low flows (see above) extended to the full suite of flows recorded, most especially for riffles (R^2 = 0.76). The limited relationships between velocity and low flow for this site alluded to above, were supported by the results here, although there was a moderate Q-mean velocity relationship for runs (Table 6.6). For the two sites subjected to the most extreme low flows, relationships between mean water depth and discharge were indisputable in all instances (also see above), and strongest overall for runs (Riviersonderend: R^2 = 0.85

and Du Toits: R^2 = 0.93). Similarly, strong dependencies of mean velocity on discharge were found for riffles and, to a greater extent runs (R^2 values of 0.84 and 0.94), at the same sites.

Table 6.6 Relationships between average depth (m), average velocity (m s^{-1}), and discharge. The best fit of a linear, logarithmic (natural), power or exponential function is presented. Trends (↑ or ↓) in average depth or velocity with a decrease in discharge are indicated. Strong relationships ($R^2 \geq 0.75$) are shaded.

SITE AND CROSS-SECTION TYPE	*n*	AVERAGE DEPTH (m) Trend with ↓ Q	Equation	R^2	AVERAGE VELOCITY (m s^{-1}) Trend with ↓ Q	Equation	R^2
All sites combined							
Riffles and runs combined	96	↓	$y = 0.208x^{0.289}$	0.272	↓	$y = 0.361x^{0.388}$	0.245
Riffles	48	↓	$y = 0.168x^{0.251}$	0.325	↓	$y = 0.319x + 0.229$	0.461
Runs	48	↓	$y = 0.259x^{0.328}$	0.348	↓	$y = 0.276x^{0.472}$	0.475
Individual sites							
EL							
Riffles and runs combined	24	↓	$y = 0.372x + 0.094$	0.114	↓	$y = 0.217x + 0.112$	0.021
Riffles	12	↓	$y = 0.140x + 0.111$	0.104	↓	$y = 0.452x + 0.115$	0.223
Runs	12	↓	$y = 0.581x^{0.675}$	0.766	↑	$y = 0.109e^{-0.192x}$	0.010
MO							
Riffles and runs combined	24	↓	$y = 0.222x^{0.436}$	0.365	↓	$y = 0.224e^{0.575x}$	0.106
Riffles	12	↓	$y = 0.190x^{0.424}$	0.761	↓	$y = 0.123x + 0.330$	0.181
Runs	12	↓	$y = 0.260x^{0.448}$	0.381	↓	$y = 0.149e^{0.855x}$	0.603
DU							
Riffles and runs combined	24	↓	$y = 0.215x^{0.375}$	0.743	↓	$y = 0.473x^{0.330}$	0.372
Riffles	12	↓	$y = 0.175x^{0.314}$	0.661	↓	$y = 0.718x^{0.400}$	0.606
Runs	12	↓	$y = 0.264x^{0.435}$	0.933	↓	$y = 0.312x^{0.261}$	0.841
RI							
Riffles and runs combined	24	↓	$y = 0.211x + 0.106$	0.528	↓	$y = 0.502x^{0.451}$	0.430
Riffles	12	↓	$y = 0.200x + 0.077$	0.702	↓	$y = 0.518x + 0.262$	0.830
Runs	12	↓	$y = 0.307x^{0.291}$	0.851	↓	$y = 0.418x^{0.645}$	0.941

Generally weaker relationships between maximum depth and maximum velocity, and discharge magnitude were observed (on the basis of the data presented in Tables 6.2 and 6.3), and are not discussed further here.

Effects of low flows on cross-channel proportions of very shallow and zero-velocity areas

Minima for depth and velocity were not particularly useful indicators of hydraulic response to low flows (see above). However, an assessment of the proportion of wetted cross-section exhibiting extremely shallow waters (d ≤ 0.05 m) and/or extremely low to zero flow conditions (mean column velocity ≤ 0.01 m s^{-1})

provided an informative way of assessing changing habitat conditions for invertebrates under different low flow regimes. Time series for (a) depth and (b) velocity, for the full study duration, are presented separately for riffle and run transect biotopes at the sites (Figures 6.8-6.11). Complementary results based on direct analysis of the relationships between the two derived hydraulic measures and discharge (Table 6.7) also are discussed here.

Temporal changes in proportions of shallow and non-flowing habitat

Under an entirely natural flow regime (Elands - Figure 6.8), sections of very shallow water were present in riffles during the dry season (even at elevated discharges) with similar patterns for different riffles within the same reach (Figure 6.8a; range in $d \leq 0.05$ m: 8-25%). As in runs, which were more variable in trend than riffles and had less shallow water habitat (max = 10%), the greatest proportion of water below 0.05 m did not necessarily occur in the month of lowest flow (see also Table 6.7). Proportions of non-flowing water occurred across both riffles and runs, with clear natural variability between cross-sections in both instances (Figure 6.8b). There was no relationship between month and maximum (17% – riffle; 18% - run) proportion of zero-velocity habitat. For both cross-section types, there were months where the full transect width was discernibly flowing.

Comparison of riffles under natural and unnatural low flows at the Molenaars site (Figure 6.9) showed that very shallow water was present in both instances, throughout the study, declining to a minimum of 8%. Although control and impact riffles displayed a similar proportion of shallow water prior to flow diversion, there was an unmistakable reduction in deep water for the impacted riffle (with an increase in extremely shallow areas to 37%; Figure 6.9a). The pattern recorded for runs was highly similar with a substantial increase in shallow water habitat at extreme low flows, though to an expected lower proportion than for riffles (up to 29%). The effect of extreme low flows on low-velocity habitat was less evident than for depth (Figure 6.9b). For riffles, at least 92% of flowing water ($v > 0.01$ m s^{-1}) remained over the full suite of discharges measured, with the maximum percentage of standing water recorded outside of months of lowest flow. For runs, maximum proportions of non-flowing habitat for control and impact runs of 12% and 17%, respectively, occurred at lowest flows (Figure 6.9b).

With greater flow diversion to well below natural minima, at the Du Toits site, the proportion of shallow water across riffles was extremely high, at 72 to 51% from February-March (Figure 6.10a), compared with 19 to 14% at natural peak low flows. Clearly, however, riffles are naturally shallow at the site (Table 6.2). For runs, in contrast, naturally at least 72% of the channel was deeper than 0.05 m over the dry season (Figure 6.10a). Extreme flows increased the proportion of very shallow water to a maximum of 67% in February (cf. 28% for the control), marginally below that of the impacted riffle. Although few riffle sections were not flowing under the natural low flow regime (Figure 6.10b), an increase in zero-flow habitat to 30% was brought about by discharge diversion. Only 12% of the control run experienced no-flow conditions

during the study. Although a modest increase in non-flowing water occurred with manipulated flow reduction, it was still below the figure of 33% attained under natural discharges (Figure 6.10b).

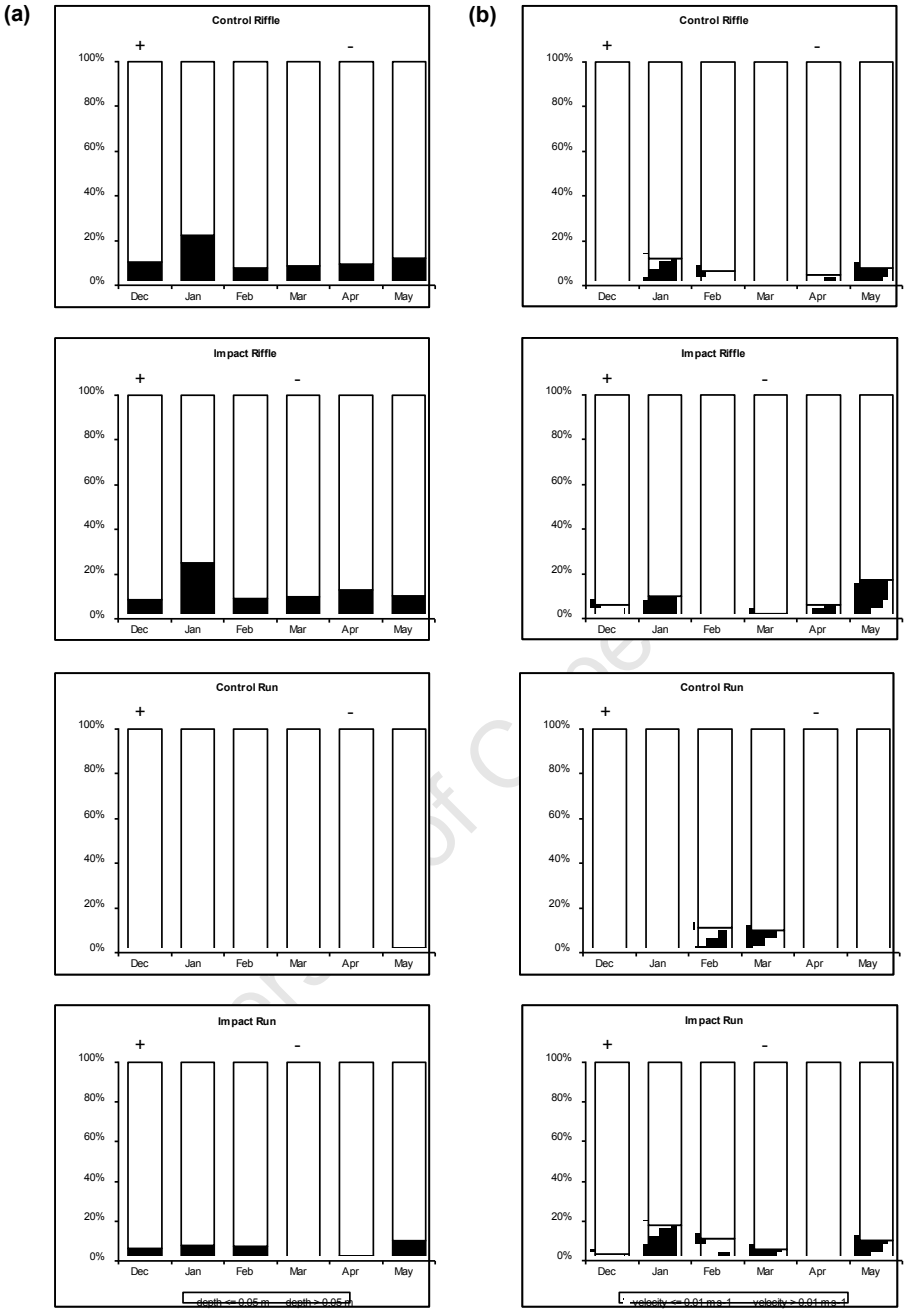


Figure 6.8 Changes in the relative proportions of (a) extremely shallow (depth ≤ 0.05 m) and (b) non-flowing (velocity ≤ 0.01 m s^{-1}) water with discharge, for the Elands site. Riffle and run transect biotopes from the two locations were treated separately. + and - indicate the months of maximum and minimum Q_{inst}, respectively.

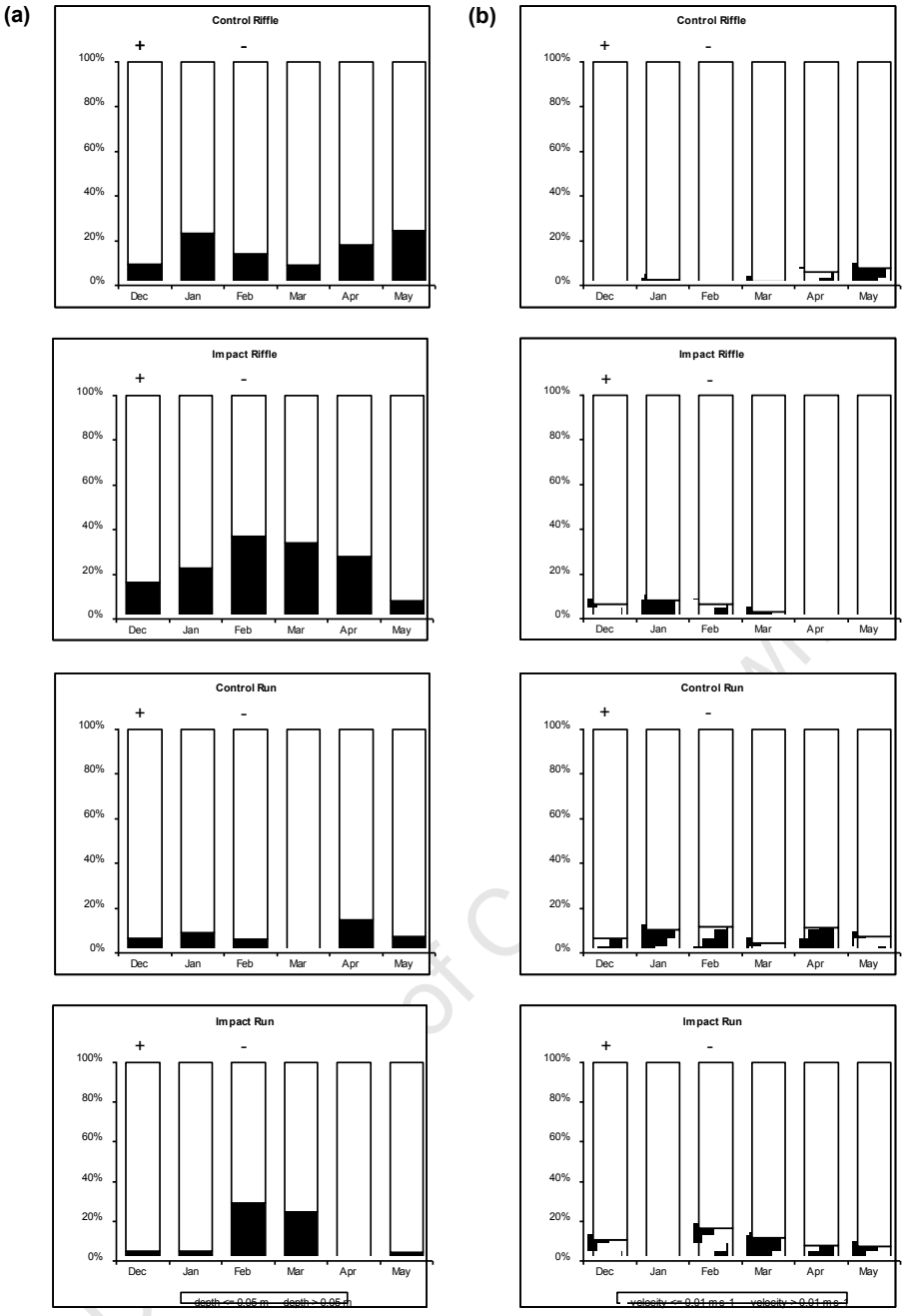


Figure 6.9 Changes in the relative proportions of (a) extremely shallow (depth ≤ 0.05 m) and (b) non-flowing (velocity ≤ 0.01 m s^{-1}) water with discharge, for the Molenaars site. Maximum (+) and minimum (-) Q_{inst}.

A similarly high diversion of flow for the Riviersonderend site did not trigger any discernible response for riffles, with February and March control figures for d ≤ 0.05 m (max: 54%) exceeding impact ones (Figure 6.11a). The data in Table 6.7 showed a stronger Q-depth relationship than suggested by this result. The proportion of shallow water was generally lower in runs, as envisaged, reaching a maximum of 23% at naturally lowest discharges. Extreme low flows transformed a markedly higher proportion of width to shallow habitat, with values of 29% and 56% obtained for the impact phase (Figure 6.11a). Markedly deeper water existed with the onset of autumn higher flows. The relatively high percentage of riffle sections at zero

velocity in all months under natural flows was not similarly sustained for the impact riffle (Figure 6.11b). The maximum proportion of non-flowing riffle cross-section (41%), however, was found at the lowest discharge. At least 78% of the run profile was flowing, showing a stable natural pattern among months. In contrast, extreme flows produced a dramatic decline in velocities (see above discussion for other evidence), with more than 70% of the run cross-channel ceasing to flow (in Mar; Figure 6.11b).

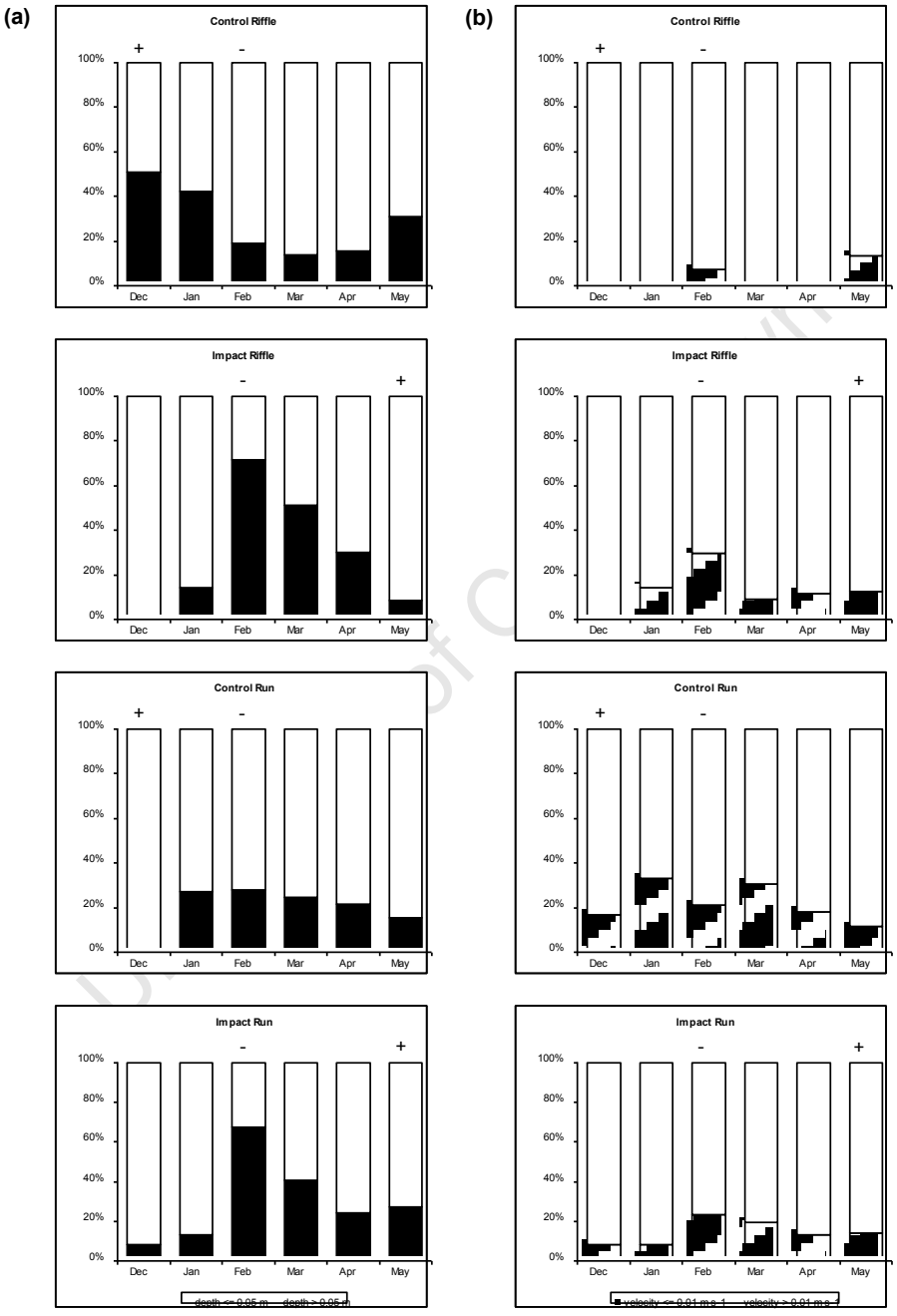


Figure 6.10 Changes in the relative proportions of (a) extremely shallow (depth ≤ 0.05 m) and (b) non-flowing (velocity ≤ 0.01 m s^{-1}) water with discharge, for the Du Toits site. Maximum (+) and minimum (-) Q_{inst}.

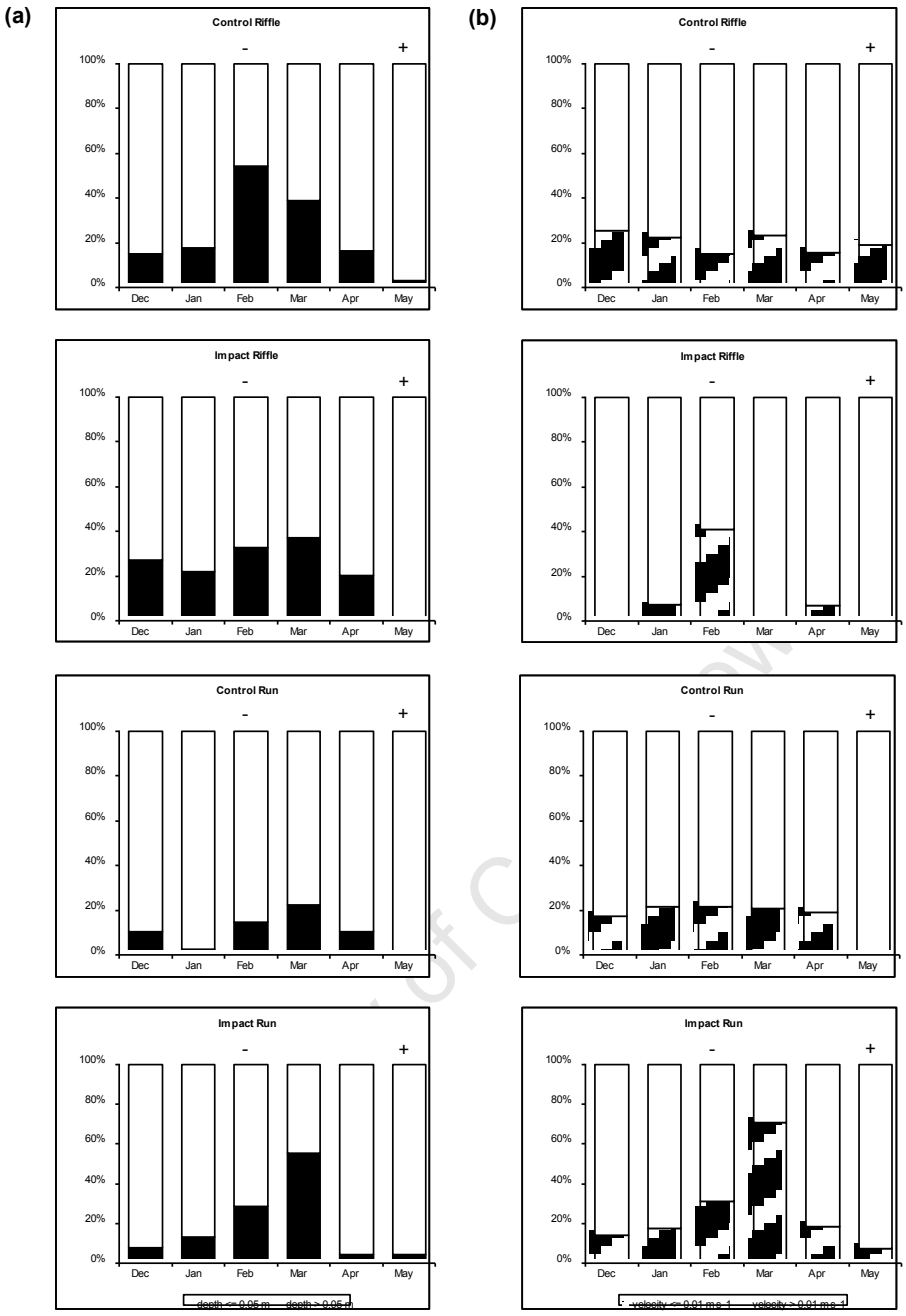


Figure 6.11 Changes in the relative proportions of (a) extremely shallow (depth ≤ 0.05 m) and (b) non-flowing (velocity ≤ 0.01 m s^{-1}) water with discharge, for the Riviersonderend site. Maximum (+) and minimum (-) Q_{inst}.

Direct relationships between shallow and non-flowing physical habitat, and discharge

The trend between discharge and the percentage of very shallow or non-flowing water was primarily a negative, weakly to moderately non-linear one for all sites combined, as well as for all experimental sites. For the experimental locations, as discharge decreased, there was a noticeable increase in shallow habitat and/or habitat of zero velocity (Table 6.7). In direct contrast, for the control site, the relationship was weakly positive or undetectable. Extreme low flows were more influential in creating shallow than non-flowing habitat, on the basis of the strengths of individual relationships. Independent treatment of riffle and run

cross-sections generated better fit results. The greatest decline to very shallow water (and strongest trend overall) was experienced in runs in the Du Toits reach (R^2 = 0.75), followed closely by both riffles and runs in the Riviersonderend River. The most detectable increase in standing water was found for the latter site (R^2 = 0.58), principally attributable to abnormally low flows.

Table 6.7 Relationships between discharge and the percentage of wetted cross-section of (a) depth ≤ 0.05 m and (b) velocity ≤ 0.01 m s^{-1}. The best fit of only a linear or natural logarithmic function is presented, due to occasional zero values. Increases (↑) or decreases (↓) in the proportion of shallow or non-flowing water with a decrease in discharge are indicated. The single strong relationship ($R^2 \geq 0.75$) is shaded.

SITE AND CROSS-SECTION TYPE	*n*	DEPTH ≤ 0.05 m (%)			0.6-VELOCITY ≤ 0.01 m s^{-1} (%)		
		Trend with ↓ Q	Equation	R^2	Trend with ↓ Q	Equation	R^2
All sites combined							
Riffles and runs combined	96	↑	y = -11.019Ln(x) + 4.457	0.274	↑	y = -4.970Ln(x) + 5.084	0.111
Riffles	48	↑	y = -10.361Ln(x) + 9.397	0.251	↑	y = -3.309Ln(x) + 4.256	0.071
Runs	48	↑	y = -11.677Ln(x) - 0.483	0.348	↑	y = -6.631Ln(x) + 5.912	0.166
Individual sites							
EL							
Riffles and runs combined	24	↓	y = 9.442Ln(x) + 20.043	0.086	↓	y = 21.372x - 0.0448	0.040
Riffles	12	↓	y = 8.348Ln(x) + 23.030	0.092	↓	y = 40.549x - 5.286	0.170
Runs	12	↓	y = 41.215x - 8.079	0.392	no relationship	y = 2.1957x + 5.196	0.000
MO							
Riffles and runs combined	24	↑	y = -15.068Ln(x) + 3.175	0.317	↑	y = -2.812Ln(x) + 3.927	0.062
Riffles	12	↑	y = -14.676Ln(x) + 9.074	0.402	no relationship	y = 0.3819x + 3.2977	0.001
Runs	12	↑	y = -15.460Ln(x) - 2.724	0.484	↑	y = -5.534Ln(x) + 4.437	0.293
DU							
Riffles and runs combined	24	↑	y = -16.515Ln(x) - 4.426	0.535	↑	y = -4.267Ln(x) + 5.050	0.135
Riffles	12	↑	y = -15.774Ln(x) - 0.904	0.407		y = -6.118Ln(x) - 3.449	0.338
Runs	12	↑	y = -17.257Ln(x) - 7.949	0.754	↑	y = -25.831x + 22.983	0.094
RI							
Riffles and runs combined	24	↑	y = -9.915Ln(x) + 3.002	0.488	↑	y = -7.715Ln(x) + 5.589	0.320
Riffles	12	↑	y = -52.105x + 39.333	0.651	↑	y = -3.854Ln(x) + 8.382	0.124
Runs	12	↑	y = -10.878Ln(x) - 3.171	0.649	↑	y = -11.577Ln(x) + 2.797	0.578

6.4 IDENTIFICATION AND FLOW RELATED HYDRAULIC CHARACTERIZATION OF BIOTOPES

6.4.1 Biotope responses to low flows at transect scale

A first, coarse-scale assessment of biotope dynamics was made at cross-channel level, where cross-sections (transects) were categorized according to the visually dominant biotope (Section 3.4.1, Figure 3.7). Recognition of biotope heterogeneity across the channel, through the subjective classification of biotope patches within an individual transect (i.e. cell biotopes - Figure 3.7), enabled an assessment of any cross-channel changes in biotope composition with discharge. It was clearly necessary to address overall changes in wetted habitat (as total biotope length, TBL - representing the summation of all lengths represented by patches of different biotope type) and any shifts in the relative composition (and hydraulic character – explored in the next section) of different biotope types in concert, with the effect of flow reduction liable to be a combination of altered biotope composition and a decrease in total habitat. The assessment focused primarily on the extent of change apparent between TBL and biotope composition at highest and lowest discharges.

A first examination of the overall relationship between discharge and TBL (with both variables standardised by maxima to allow inter-site comparisons) showed a decline in physical habitat availability with flow reduction (n = 96, y = 41.336 $x^{0.178}$, R^2 = 0.62), most pronounced when TBL fell below *c.* 70% of maximum. The best fit trend was found for runs, where a similar relationship was observed (n = 48, y = 39.555 $x^{0.195}$, R^2 = 0.78). On the basis of only riffle transects, the relationship was weaker and characteristically linear (n = 48, y = 0.386x + 58.442, R^2 = 0.60). The following sections address responses for riffle and then run transects in greater detail, focusing on flow-related dynamics in transect TBL and cell biotope composition across transects.

Riffle transects

Throughout the range of natural discharges, the control site exhibited a fairly limited change in total available habitat as TBL across riffle transects (Figures 6.12a-d), from an overall minimum of 7.6 m at the peak of the dry season, to a maximum of 12.0 m in the highest flow months. Between-riffle variability in natural sensitivity to low flow regime was apparent (Figure 6.12a cf. 6.12b). The disparity was probably in part a result of observed differences in riffle physical structure, with the impact riffle forming a wider, more pronounced cobble/boulder bar than the more gradually sloping control riffle. The results also suggested possibly a marginally higher Q_{inst} in May than December, pointing to limited precision in low flow measurement (the Elands low flows fluctuated within a narrow envelope of 0.2-0.4 $m^3 s^{-1}$; Chapter 4). In addition, the proportional representation of different biotope types varied despite the relatively stable low flow regime (Figures 6.12b and 6.12d). With natural reduction in discharge to lowest levels by April, there was a distinct switch in dominance from riffles (84% in Dec) to runs (69%). Even if the May results were

out of temporal flow sequence, the dominance by run, not riffle patches as expected, at elevated discharge for both riffle cross-sections remained an anomaly that could not be explained simply through changes in mean hydraulics (Table 6.2). Patches transitional in character between riffle and run cells increased with declining discharge, probably reflecting increased patch heterogeneity at the outer edges of large patches, an increase in smaller-sized patches, and increased influence of the substratum on hydraulics. These factors all contributed to increased difficulty in visually characterizing biotopes at low flows. No detectable change in the proportions of pools and other lower energy patches was evident in response to discharge fluctuations.

Although there was no clear pattern in TBL from month to month for riffles at the Molenaars site (Figures 6.13a and 6.13c), it was consistently lowest in the month of lowest flow. There was, however, no discernible effect of natural flow on the proportional representation of cell biotopes at cross-channel scale at all except the highest discharge, when riffle cells predominated and no transitional biotopes were evident. Classification of cross-sections as riffles based on December visits was shown to hold true only in that month; riffles were the dominant cell biotope at 62% and 81%, for control and impact locations, respectively (Figures 6.13b and 6.13d). As with the Elands site, there was some evidence of flows being higher in May than December for the Molenaars River, on the basis of TBL results for riffles (as well as runs, below). Results from all other months demonstrated a fairly balanced overall co-dominance by riffle and run cell biotopes, indicating that a more 'mixed' transect type was characteristic of the reach. In contrast to 81% of maximum TBL remaining naturally mid-dry season, extreme discharge reduction left only 57% of total habitat (Figure 6.13a cf. 6.13c). Associated with habitat loss was the appearance of pool patches at riffle margins (Figure 6.13d), while at naturally low flows cell biotope composition appeared unaltered by shrinking in TBL (Figure 6.13b). The habitat loss for the impacted riffle was further related to a marked decrease in patch connectivity along the cross-section and a concomitant increase in the width of exposed cobble/boulder sections.

For the Du Toits reach (Figures 6.14a-d), with natural flow fluctuation, there was no pattern in riffle TBL beyond a decline to minimum levels (3.3 m) mid-dry season. The January outlier was a result of patches of standing water, which possibly represented water remaining from an antecedent higher discharge (Figure 6.14a). The apparent marked decrease in TBL for the impacted riffle, to 3.9 m, represented the same magnitude decrease from pre-impact levels as the control, at around 38% (Figures 6.14a and 6.14c). Examination of within-transect biotope composition, however, showed a shift towards lower energy biotopes, with the entire loss of riffle patches and an increase in the proportion of runs to 88% (Figure 6.14d). Indeed, within the entire impact location, only a few very small patches of riffle remained at extreme low flows (pers. obs.; see also below). Also in evidence was an increase in the widths of riffle bed exposed. The only measurable shift at naturally lowest discharge was a decline in riffle patches to a recorded minimum of 44% of TBL, concomitant with an increase in transitional riffle/run cells (Figure 6.14b). With a further increase in discharge in May, some riffle patches transformed to runs (Figure 6.14d).

A well developed pattern of decreasing TBL with naturally decreasing discharge was observed for riffle transects at the Riviersonderend site, from a maximum of 8.3 m to only 5.3 m (Figure 6.15a). There was no apparent effect on biotope composition of a marked increase in discharge at the start of autumn, even for the dominant cell biotope (riffle length ranged from 56-71% over the study; Figure 6.15b). The similar-sized impacted riffle showed a marginally more pronounced decline in TBL than the control, to 4.8 m, representing 58% of maximum (Figure 6.15c). Increased proportions of run patches (maximum = 62% of total) at the expense of almost all riffle habitat, as well as a first appearance of trickle run and pool biotopes, pointed more distinctly to an effect of extreme low flows (Figure 6.15d). A total of only two small patches of riffle remained during the impact phase within the flow-impacted location, with a dramatic increase in bed exposure (pers. obs.).

The observed shifts in dominance for riffle transect biotopes in response to decreasing discharge are summarised across all sites in Figure 6.16.

Run transects

The observed low variability in total biotope availability and proportions of different biotope types over time closely matched the stability of the low flow regime for runs at the Elands site (Figures 6.17a-d). Total biotope length range between 8.9-12.1 m, from the month of lowest recorded discharge to a maximum in May (Figures 6.17a and 6.17c). At the higher end of the low flow regime, a slight increase in pool patches was observed, but runs remained the dominant cell biotope throughout the study at 76-100% irrespective of discharge (Figures 6.17b and 6.17d). Areas of pool/run transition were more evident than in the case of riffles, as envisaged. The greater within-transect homogeneity observed for runs than for riffles was attributable to more even cross-channel morphology in the former case, with comparatively far fewer protruding bed elements.

At the Molenaars site, runs were more homogeneous than riffles (Figures 6.18a-d). Under the natural low flow regime, run TBL remained highly similar throughout the study period and still 88% of maximum in February. At the cell biotope level, there was consistent domination by runs (75-93% of TBL), with only a small increase in low flow biotopes (pool/run transition and standing water patches, 22% in total) at lowest natural discharge (Figure 6.18b). With discharge reduction to abnormal lows, there was a distinct decline in TBL (Figure 6.18c) to 80% of maximum (TBL was always above 95% of maximum outside of the impact phase). There was a noticeable shift overall towards lower energy biotopes, linked to the reduction in mean hydraulic values remarked upon earlier (Figure 6.18d and Table 6.3), with the entire loss of riffle patches, an increase in run cells to maximum (81%), and the appearance of areas transitional between runs and pools. Furthermore, an increase in bed exposure was observed at extreme low flows (Appendix 6.1).

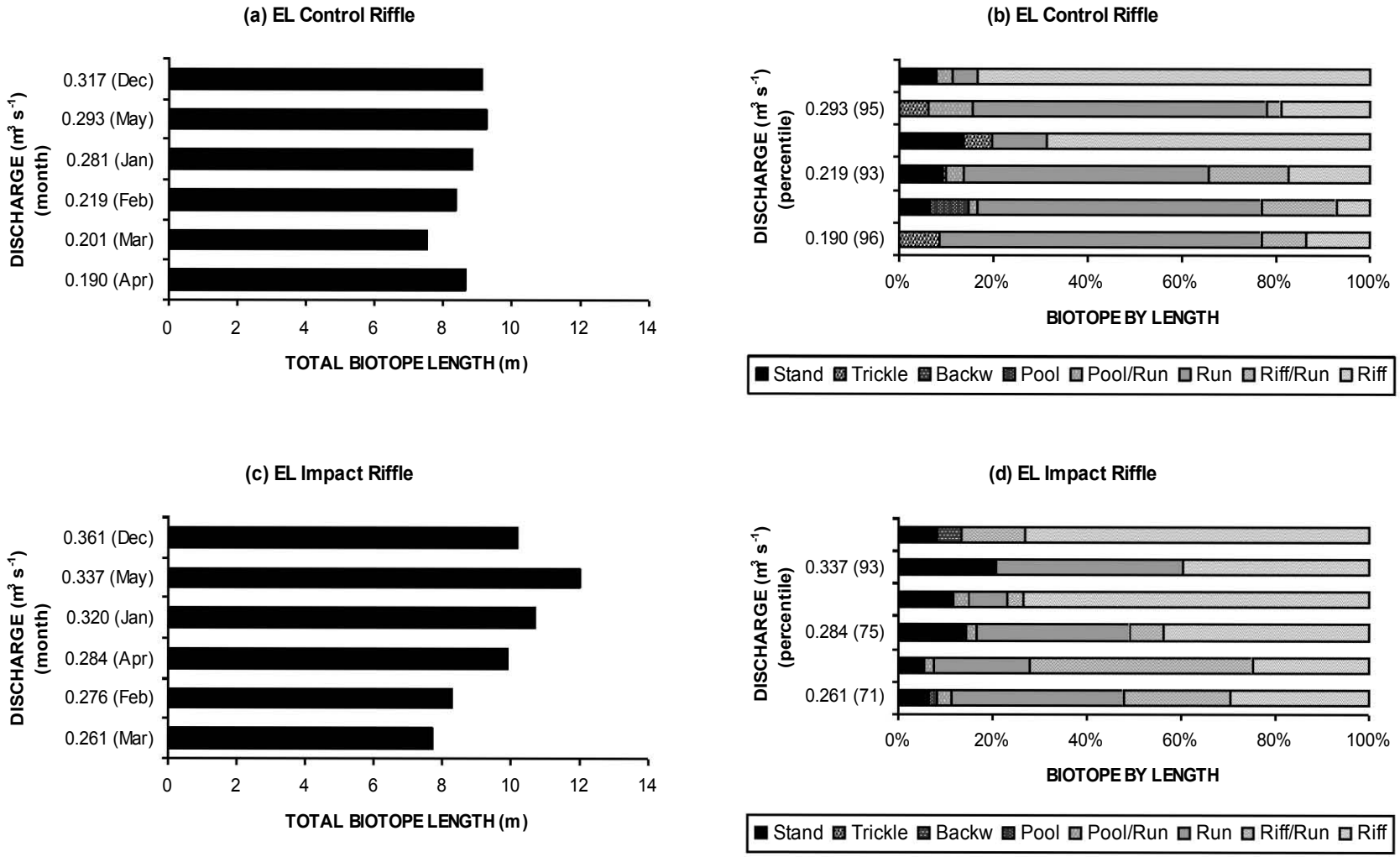


Figure 6.12 **(a) Total biotope length (m) and (b) proportions of biotope types by length (%) for riffle cross-sections in the Elands control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for riffles in the 'impact' location.** Corresponding flow percentiles (derived from monthly FDCs) and sampling months are indicated.

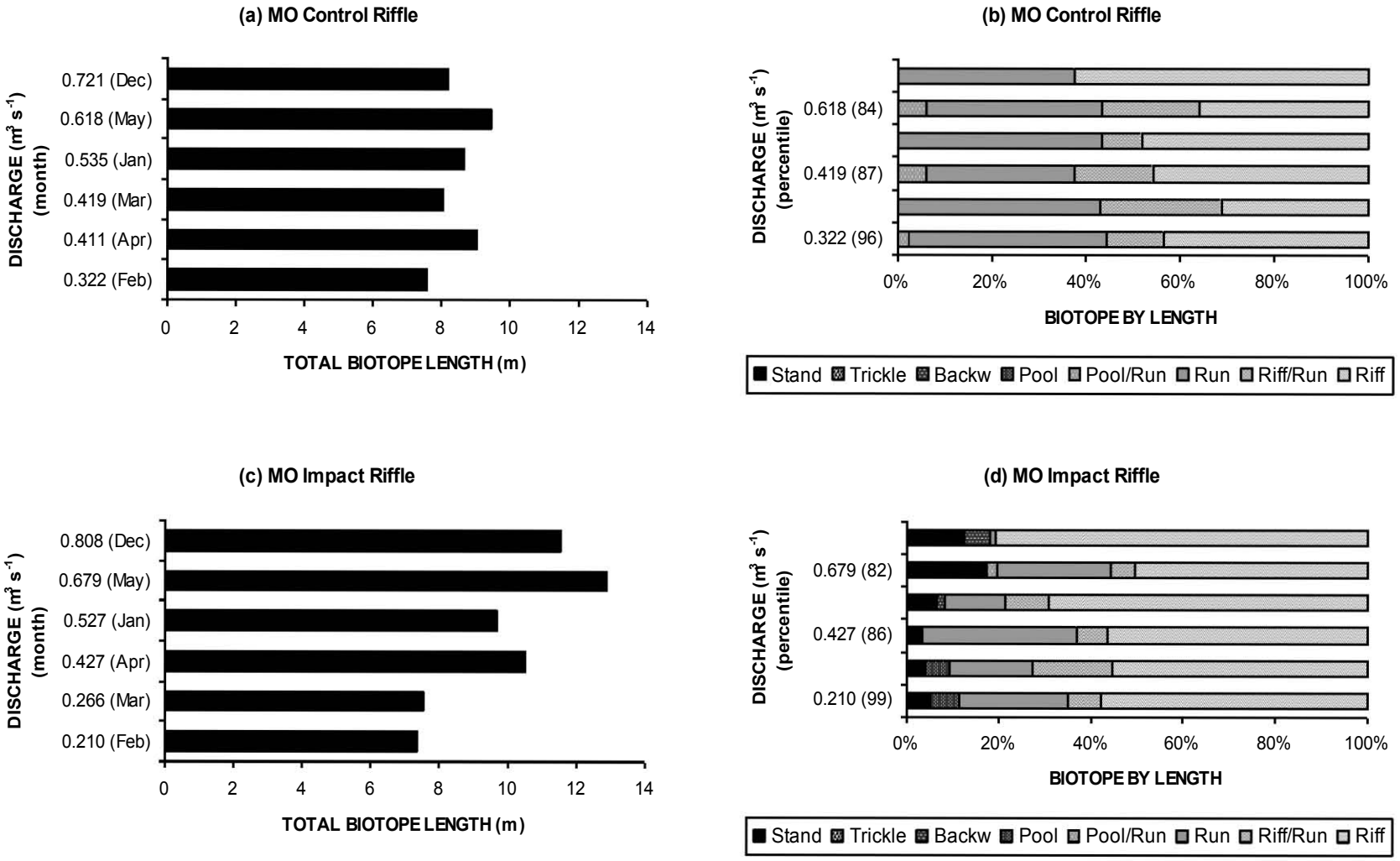


Figure 6.13 (a) Total biotope length (m) and (b) proportions of biotope types by length (%) for riffle cross-sections in the Molenaars control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for impact riffles. Corresponding flow percentiles and sampling months are indicated.

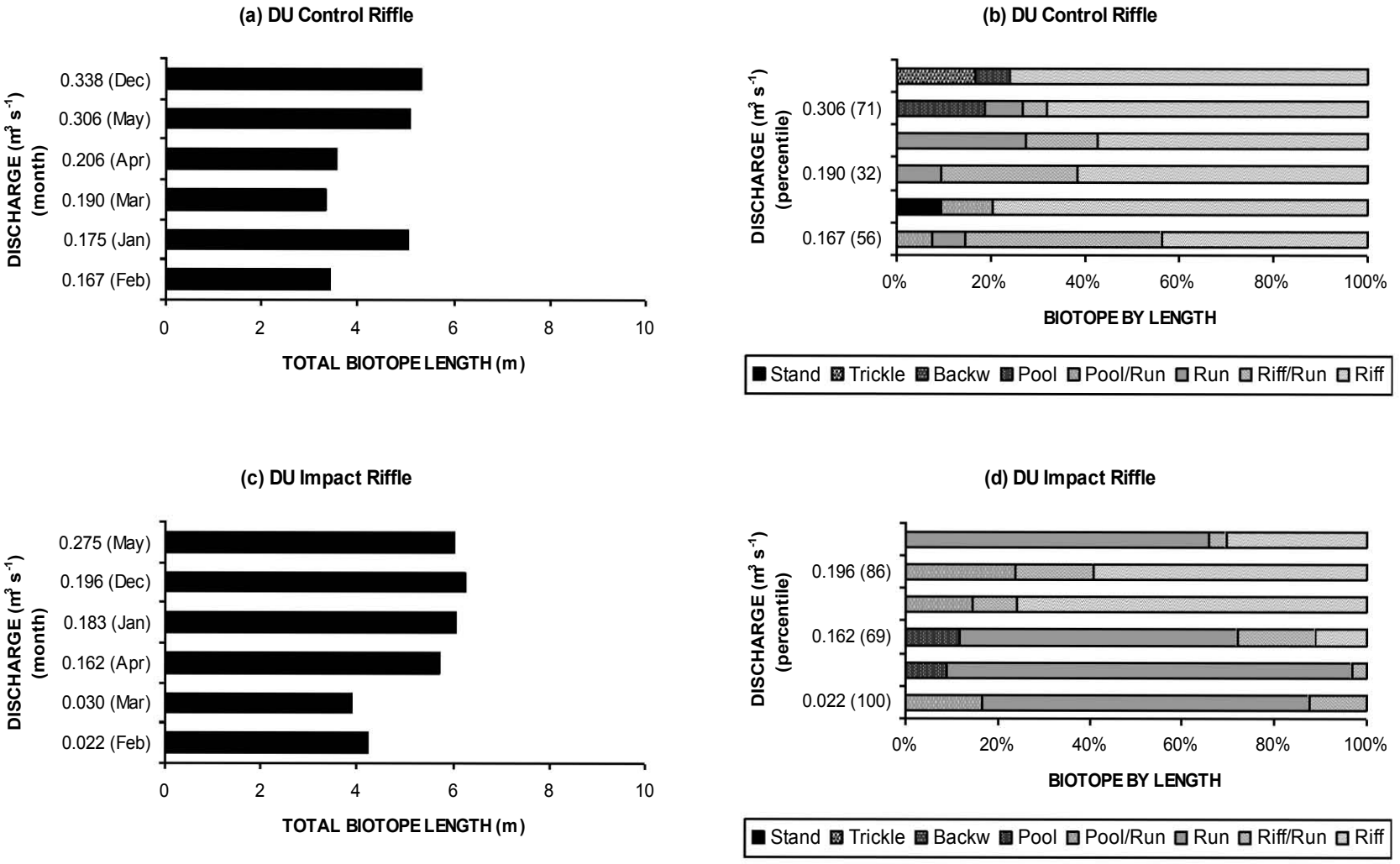


Figure 6.14 (a) Total biotope length (m) and (b) proportions of biotope types by length (%) for riffle cross-sections in the Du Toits control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for impact riffles. Corresponding flow percentiles and sampling months are indicated.

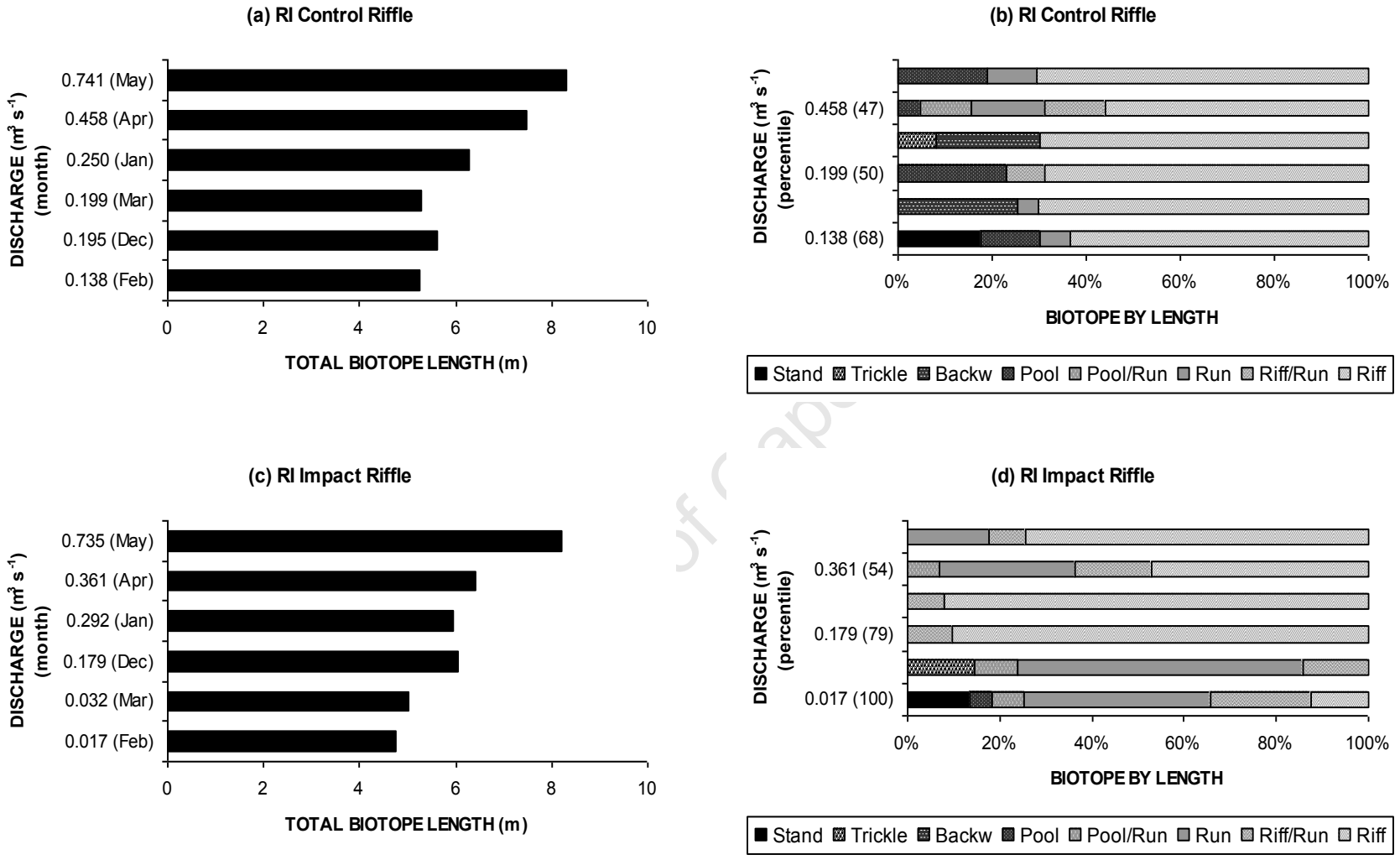


Figure 6.15 (a) Total biotope length (m) and (b) proportions of biotope types by length (%) for riffle cross-sections in the Riviersonderend control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for impact riffles. Corresponding flow percentiles and sampling months are indicated.

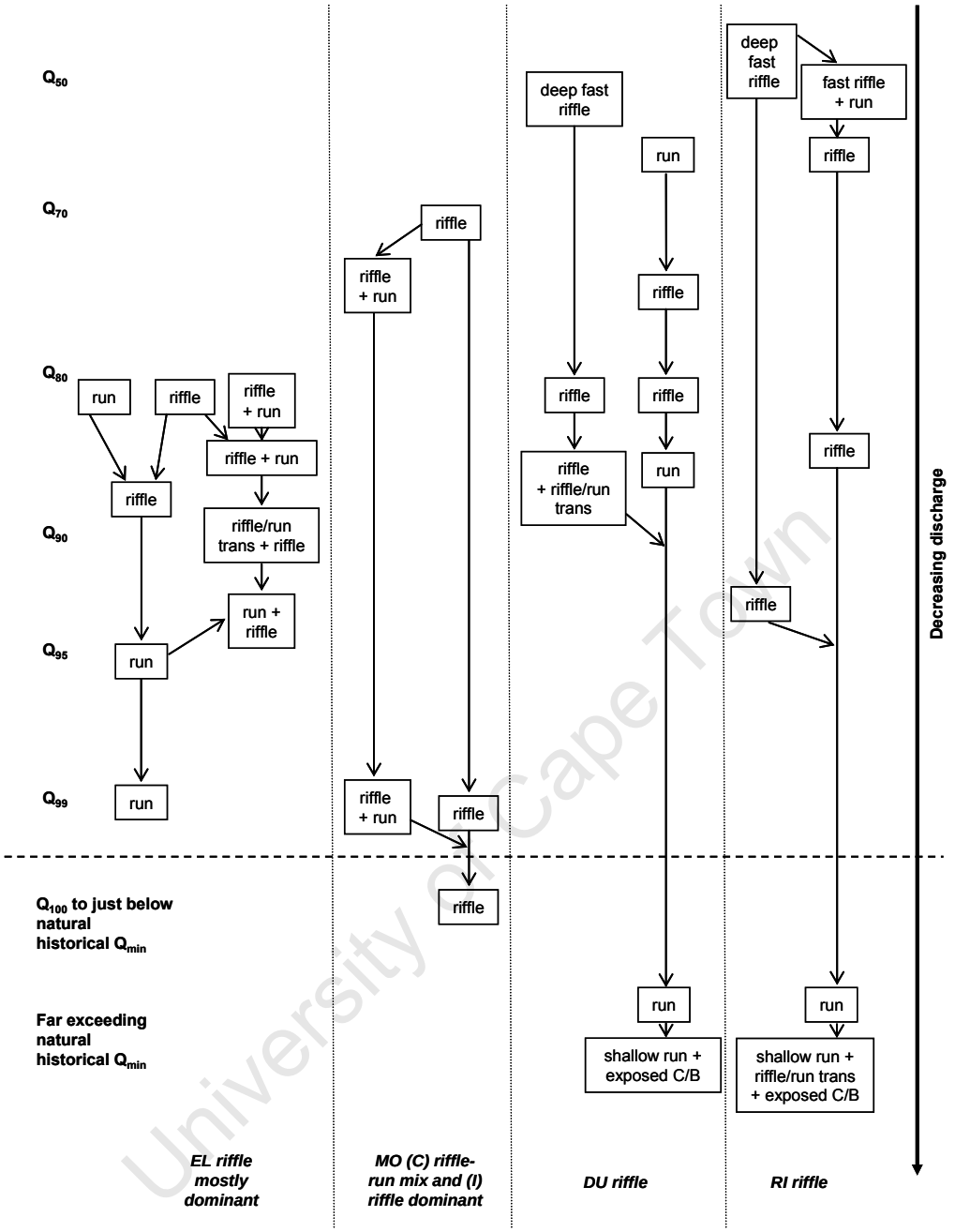


Figure 6.16 Generalised transect biotope response to discharge reduction for riffles. Corresponding flow percentiles are indicated. C – control location; I – impact location; trans – transitional biotope type; C/B – cobble/boulder.

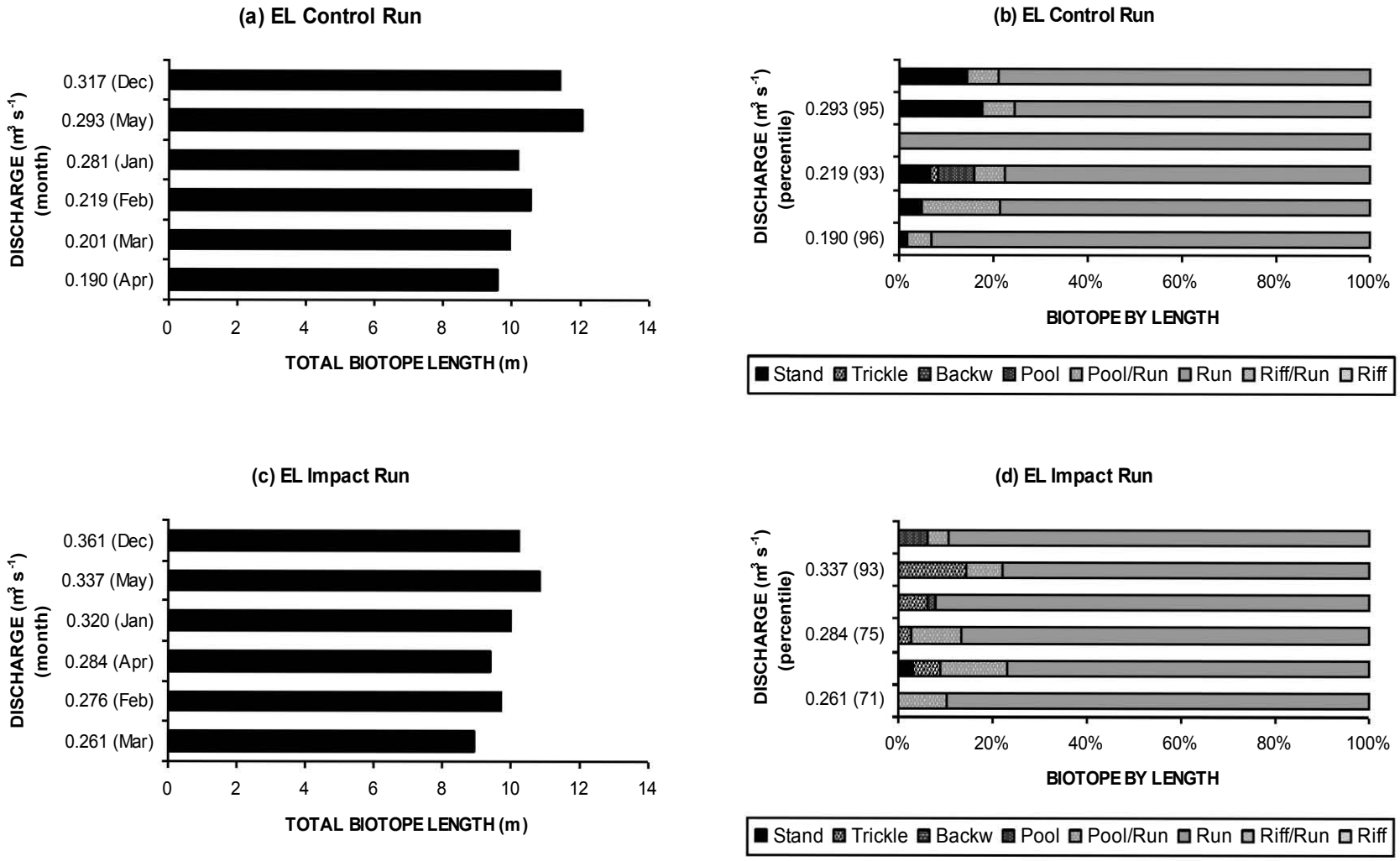


Figure 6.17 **(a) Total biotope length (m) and (b) proportions of biotope types by length (%), for run cross-sections in the Elands control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for runs in the 'impact' location.** Corresponding flow percentiles and sampling months are indicated.

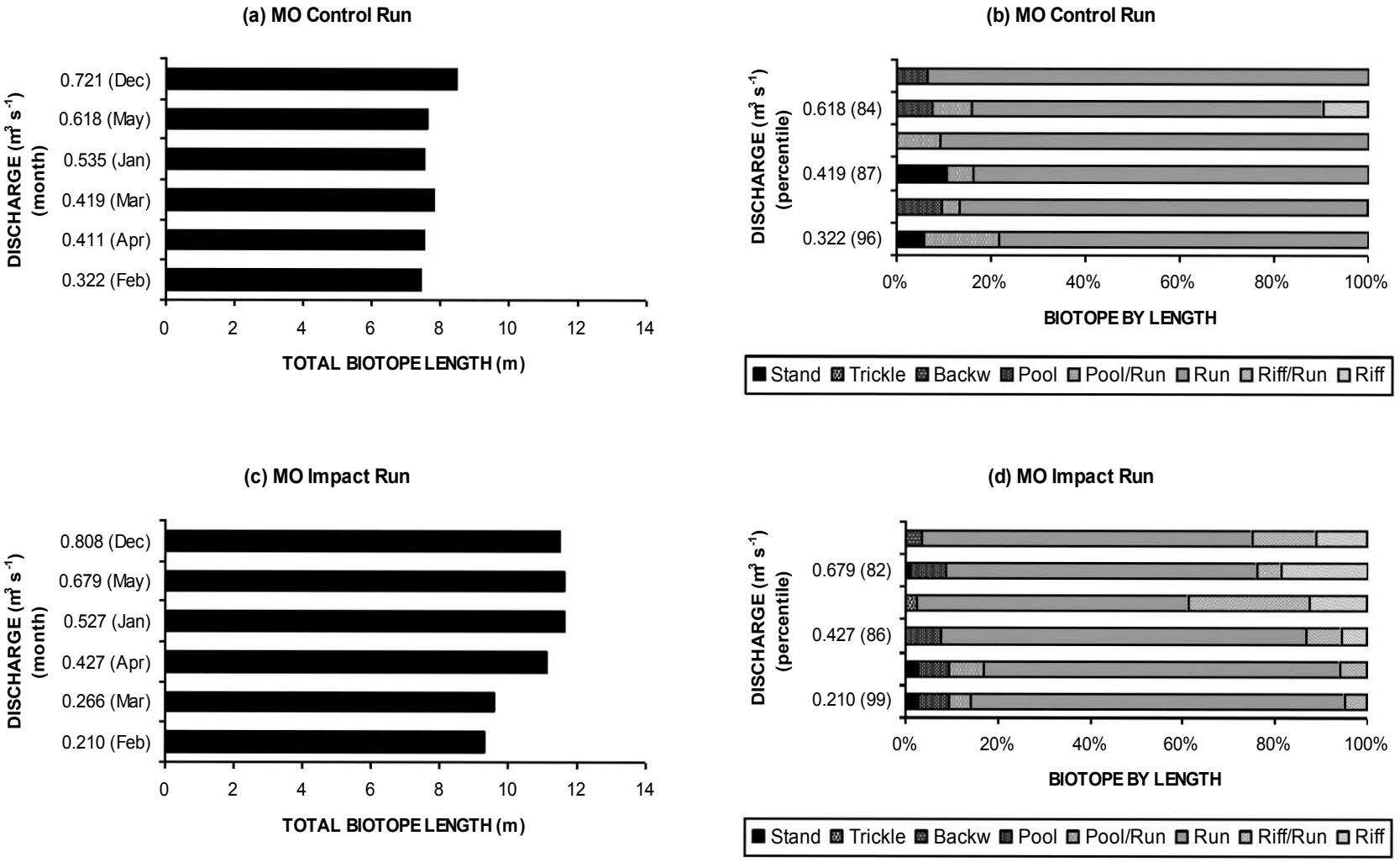


Figure 6.18 (a) Total biotope length (m) and (b) proportions of biotope types by length (%), for run cross-sections in the Molenaars control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for impact runs. Corresponding flow percentiles and sampling months are indicated.

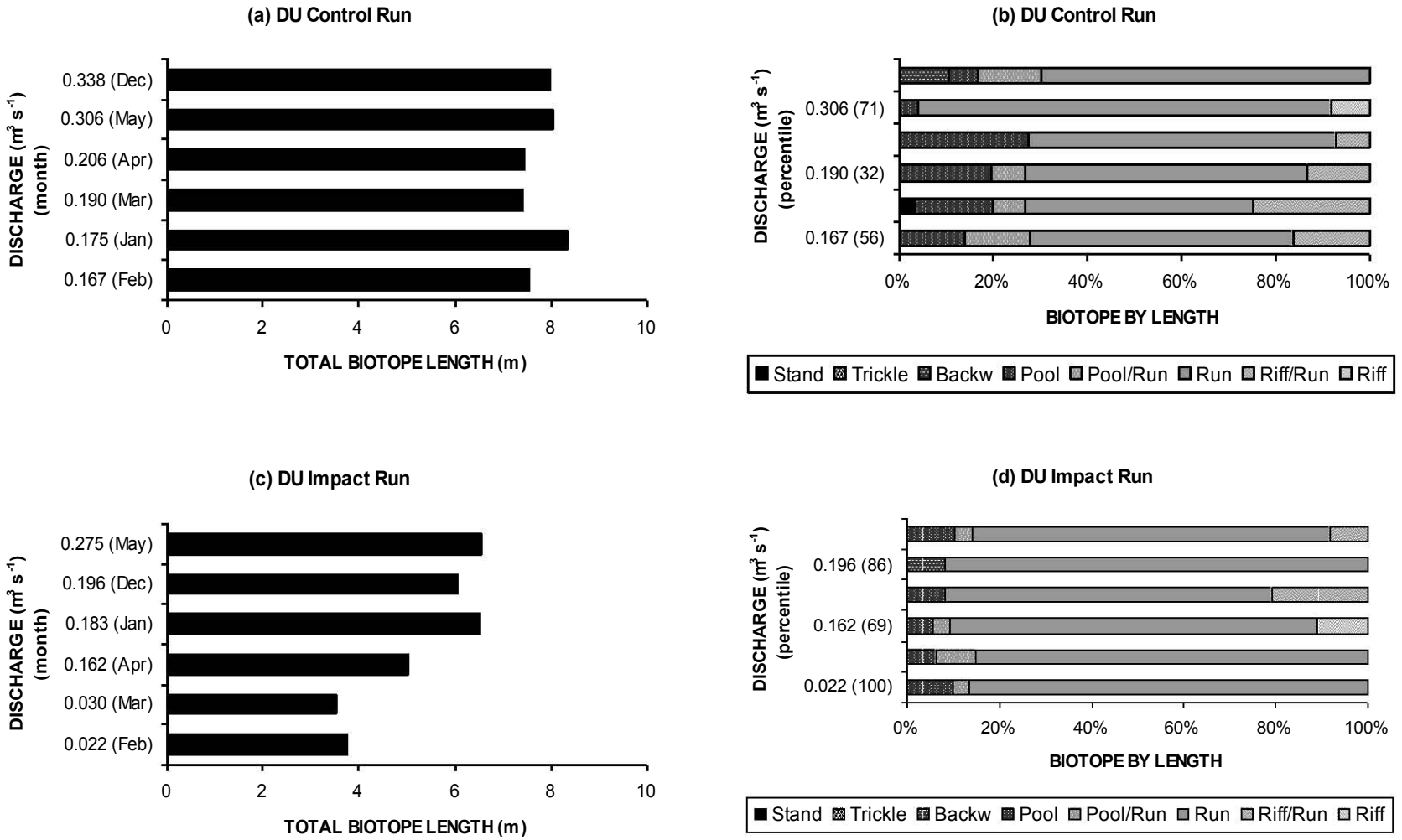


Figure 6.19 (a) Total biotope length (m) and (b) proportions of biotope types by length (%), for run cross-sections in the Du Toits control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for impact runs. Corresponding flow percentiles and sampling months are indicated.

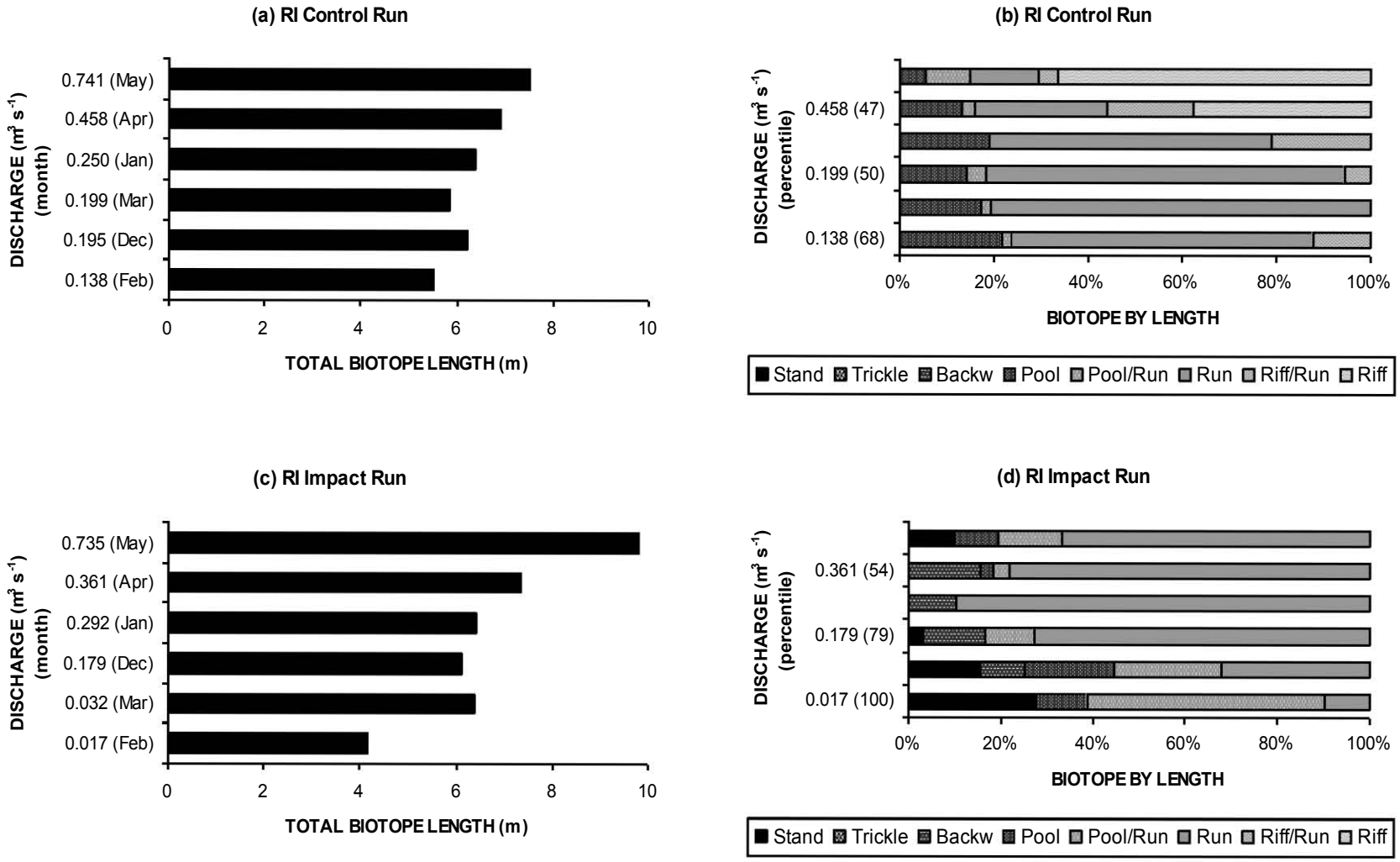


Figure 6.20 (a) Total biotope length (m) and (b) proportions of biotope types by length (%), for run cross-sections in the Riviersonderend control location, in a sequence of decreasing discharge from top to bottom, and in (c) and (d) for impact runs. Corresponding flow percentiles and sampling months are indicated.

Total biotope availability (as TBL) fluctuated within a narrow range for the Du Toits control run, consistently above or at 89% of the maximum of 8.3 m, with a gradual decrease in the proportion of the cross-section exhibiting run characteristics (Figures 6.19a and b). A high percentage of pools (primarily shallow, marginal deadwaters) were recorded compared with the Elands and Molenaars transects. At extreme low flows (Figure 6.19c) a near halving in run TBL to only 3.5 m was recorded representing a pronounced overall loss in wetted habitat. Run cell biotopes remained similarly dominant (71-92% of TBL) irrespective of the magnitude of flow change, and there was no obvious response in pools or pool/run transitional patches (Figure 6.19d). The lack of response in such biotope patches was in contrast to the situation recorded for the impacted run in the Riviersonderend reach, where several naturally deep, relatively large pools were present. The hydraulic character of the impacted run was, however, profoundly influenced by severe discharge reduction, as shown in Table 6.3 and discussed above. Moreover, there was a marked loss of habitat connectivity (Appendix 6.1).

The results of an assessment of the dynamics of runs for the Riviersonderend site are depicted in Figures 6.20a-d. A relationship between discharge and TBL was apparent, with a 27% decrease in TBL from a maximum of 7.5 m to a February minimum of 5.5 m (Figure 6.20a). For the impacted run (Figure 6.20c), the general pattern remained, but was influenced in March by an outlier, where small patches of standing water representing a backwater added to total biotope length (not recorded in Feb). With extreme flow reduction, the same percentage decrease of 58% (to 4.1 m) recorded for the impacted riffle was observed. In this case, however, comparison with the control run demonstrated the significance of this difference. In terms of within-transect biotope composition, at the lower spectrum of flows, a slight shift towards increased representation by a combination of pools (22% in Feb), pool/run transitional areas and runs was recorded (Figure 6.20b). The most marked shift in dominance was apparent with the transition to higher flows, with riffle cells replacing run patches to the extent of 66% of TBL (Figure 6.20b). Prior to the last two study months, only riffle/run transitional areas were apparent. With the natural, relatively large-scale increases in discharge recorded in autumn, and associated changes in velocity relative to depth, the cross-section was reclassified as a riffle/run transition (Apr) and then as a riffle (May) (Figure 6.21).

Under natural flows outside of the flow-reduction period, the same pattern was not reflected by the impact run in the post-impact phase, with runs remaining dominant (though increasing in depth and velocity), due to the naturally deeper character of the cross-section (Figure 6.20d and Table 6.3). Of the experimental sites, the most pronounced shift in composition was recorded for this site, for which experimental flow reduction was greatest, with biotope dominance entirely altered for the full duration of the experimental phase. Runs transformed from being by far the dominant cell biotope at natural discharges (a range of 67-90% of TBL) to being only the third most abundant biotope type. Pool/run transition areas emerged as dominant, attaining 51% at 0.017 $m^3 s^{-1}$, followed by isolated patches of standing water (28%) Figure 6.20d). In stark contrast,

runs were less than 10% of TBL. Hence, the impacted run was reclassified as a pool/run for the duration of the impact phase. Also noteworthy was the increased dissection of the river bed (Appendix 6.1).

Across all sites, the observed shifts in dominance for run transect biotopes in response to decreasing discharge are summarised in Figure 6.21.

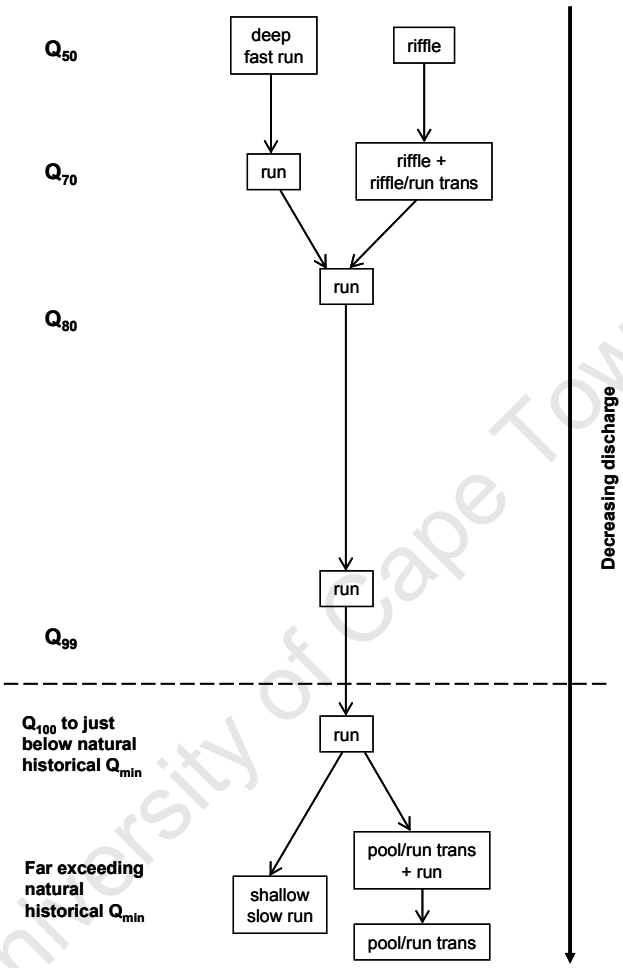


Figure 6.21 Generalised transect biotope response to discharge reduction for runs. Corresponding flow percentiles are indicated. Trans – transitional biotope type.

6.4.2 Flow-related characterization of hydraulic biotopes

Biotope discreteness and hydraulic character

A first objective classification of visually identified hydraulic biotopes, at patch scale, across all the sites and discharges (i.e. aggregate analysis, 'aggr') (Table 6.8), coupled with corresponding summary statistics (Appendix 6.3) allowed an assessment of their validity as independent, robust units. It also provided a first understanding of the core variables (i.e. depth, mean column velocity, near-bottom velocity, substratum median particle size; Section 3.4.4) and derived hydraulic variables that most discriminated among the

different hydraulic biotopes, and of which indices best described the character of individual biotope types. The hydraulic variables are described in Section 3.4.4.

Table 6.8 Results of forward stepwise discriminant analysis for objective classification of all hydraulic biotopes recorded in the field, based on an aggregate data set. Both core and derived hydraulic variables were included in the analysis. Model variables with greatest discriminatory power are shaded.

MODEL			
***n* = 1935**	**Wilks' Lambda = 0.410**	**Approx. F (63, 10 814) = 29.420**	***P* < 0.000**
Model variables (*n* = 9)	**Partial Wilks' Lambda**	**F-remove (7, 1919)**	**p-level**
Depth	0.932	19.922	0.000
Fr	0.959	11.599	0.000
$SUBd_{50}$	0.969	8.649	0.000
NBV	0.970	8.495	0.000
VD_{ratio}	0.982	5.137	0.000
Re	0.987	3.617	0.001
R_{rel}	0.990	2.883	0.005
TI	0.994	1.737	0.096
RE	0.995	1.262	0.266

Abbreviations: depth (d); mean column velocity (0.6V); near-bottom velocity (NBV); velocity: depth ratio (VD_{ratio}), median particle size ($SUBd_{50}$); Froude number (Fr); Reynolds number (Re); shear velocity (v_*); Roughness Reynolds number (Re_*); relative exposure (RE); turbulence index (TI); and relative roughness (R_{rel}).

Discrimination among the eight types of hydraulic biotopes encountered, using a model based on a combination of nine core and derived hydraulic variables, was highly significant (n = 1935, Wilks' Lambda = 0.410, F = 29.420, P < 0.0001), with depth (d) and Froude number (Fr) contributing most overall to inter-biotope discrimination. The strong correlation between shear velocity (v_*) and roughness Reynolds number (Re_*) rendered the latter variable redundant for all analyses conducted. The decreased reliability of the velocity profile and associated instability in microhydraulics observed at extremely shallow depths relative to substratum particle size, at very low discharges, probably explained why v_* was not an adequate discriminator for the model (in 47 cases, all at d < 0.06 m, negative shear velocities were encountered). High tolerance values for mean column velocity (0.6V) and velocity shelter similarly resulted in their exclusion from the model.

The results of canonical analysis indicated that despite a high number of model variables and weak individual discriminatory power (Partial Wilks' Lambda values above 0.9), the first three discriminant functions (roots) were highly significant (Table 6.9). The first function, weighted most heavily by Fr and then NBV (Table 6.10), accounted for 82% of the explained variance and hence, discriminatory power. Depth and to a lesser extent Reynolds number (Re) contributed most to the second function, and together with the first discriminant function, explained 97% of total observed variance. A lesser, but still significant

contribution to differences among biotopes was largely due to velocity: depth ratio (VD_{ratio}). Examination of the means of the canonical variables for the three discriminant functions for individual biotopes (Table 6.11) lent further support for the combinations of variables most responsible for the separation of biotopes into hydraulically distinct types.

Table 6.9 Results of Chi-square tests with successive roots removed, for the model described in Table 6.8.

ROOTS REMOVED	EIGENVALUE	CANONICAL R	WILKS' LAMBDA	χ^2	DF	*P*
0	0.983	0.704	0.410	1715.407	63	0.000
1	0.179	0.390	0.814	397.131	48	0.000
2	0.025	0.156	0.959	79.794	35	0.000
3	0.009	0.096	0.983	32.288	24	0.120
4	0.006	0.075	0.993	14.352	15	0.499
5	0.002	0.043	0.998	3.511	8	0.898

Table 6.10 Standardised coefficients for canonical variables (core and derived hydraulic indices) for the significant roots. The model is described in Table 6.8.

VARIABLE	ROOT 1	ROOT 2	ROOT 3
NBV	0.484	-0.138	0.190
Depth	0.113	1.111	0.133
Fr	0.723	0.408	0.145
VD_{ratio}	-0.311	-0.214	-0.701
$SUBd_{50}$	0.153	0.409	-0.314
Re	0.126	-0.507	-0.150
TI	-0.130	0.258	-0.180
R_{rel}	-0.076	-0.074	-0.377
RE	0.098	0.042	-0.122
Eigenvalue	0.983	0.179	0.025
Cumulative Proportion Variance	**0.816**	**0.965**	**0.986**

Separation among biotopes was found to be driven along two main axes of (i) increasing turbulence (Fr) and velocity (reflected by NBV, which followed a similar trend to 0.6V), together effectively representing 'hydraulic energy', and (ii) increasing water depth. The ratio of mean column velocity to depth further contributed to the discreteness of individual biotopes. The first discriminant function most clearly differentiated between pool environments (e.g. backwaters, standing waters, main channel pools) and other biotopes. Froude numbers, particularly, differentiated among low to high energy biotopes, ranging from $\bar{x}$ = 0.009 ± 0.062 for pools (and even lower for backwaters and standing waters) to a maximum mean across all biotopes of 0.507 (SD = 0.353) for riffles (Appendix 6.3). In addition to high Fr values, riffles, followed closely by the more variable riffle/run transition patches, were characterized by highest median VD_{ratio}

(4.074 s^{-1}) (Appendix 6.3). Runs were intermediate in Fr numbers ($\bar{x}$ = 0.155 ± 0.134) and velocities, and were most distinguished from all other biotopes by their greater mean and median depths, of 0.20 m and 0.18 m, respectively. Depths were particularly low for all pool types (most pools represented characteristically shallow marginal slackwaters), and similarly a little higher for transitional biotopes and riffles (Appendix 6.3). Trickle runs were of complex hydraulic character, due to the protrusion of the coarser substrata from the water surface generating hydraulically rough flow (Appendix 6.3). Separated most from other biotopes by the second and third discriminant functions, they exhibited very low depths (median = 0.03 m), Re (median = 40), and v_* (median = 0 m s^{-1}) figures (similar to those of standing waters), but high relative exposure and relative roughness (medians of 0.108 and 9.3, respectively).

Table 6.11 Means of canonical variables for pre-defined hydraulic biotopes. The corresponding model is given in Table 6.8.

GROUP	ROOT 1	ROOT 2	ROOT 3
Trickle Run	-1.121	-1.272	-1.561
Run	-0.303	0.477	-0.009
Riffle	1.332	-0.217	0.052
Pool	-1.332	-0.486	0.110
Pool/Run Trans	-1.085	-0.057	-0.020
Riffle/Run Trans	0.288	-0.178	-0.352
Backw	-1.447	-1.027	0.112
Stand	-1.553	-1.590	0.005

Classification of hydraulic biotopes based on the above model proved moderately successful, demonstrating sufficient robustness of most biotope types, most notably runs at 85% (Table 6.12) – a threshold cutoff of 65% was adopted *a priori* for evaluating classification success, on the basis of similar work by Jowett (1993) and Wadeson (1996). Misclassification of backwaters and standing waters as pools was understandable, given the highly similar hydraulic environments characteristic of these biotopes (Table 6.12 and Appendix 6.3). The first two biotopes were better differentiated by differences in physical structure, including their degree of isolation from the flowing channel (as explained in Table 3.5). Trickle runs tended to be misclassified as other lower energy biotopes, despite some classification with riffles due to hydraulically rough flow. It was clear from the predominant misclassification of both riffles and pools as runs, that the category 'runs' represented hydraulically too broad a biotope type. Turbulence though maximum for riffles, also occurred in runs. The latter biotope exhibited marginally higher turbulence than patches of riffle/run transition, while lower energy biotopes showed no turbulence, as well as some influence of upstream boulder/bedrock elements (i.e. hydraulic refuges; Table 6.13). Furthermore, the classification results showed that neither transitional biotope could be readily characterized (Table 6.12). Most likely, the transitional biotopes reflected actual patches of hydraulic transition between physically adjacent biotopes, rendering them difficult to classify as either neighbouring biotope in the field. An analysis of the percentage of cases in the discriminant analysis representing an influence of upstream larger bed elements showed that the

greatest impact was experienced by pool/run transition areas (22.1%, Table 6.13). Probably, this largely explained the difficulty in visual classification of such patches. Recoding of both transitional biotopes as runs (based on the misclassification results of Table 6.12) marginally improved the classification success of runs to 88%, while reducing it for riffles and pools. Based on these findings, the two transitional biotopes were treated as independent biotopes in subsequent analyses.

Table 6.12 Classification matrix based on the discriminant analysis summarised in Table 6.8. Hydraulic biotopes to which misclassified cases commonly were allocated are shaded.

BIOTOPE	PERCENT CORRECTLY CLASSIFIED	PERCENT OF CASES MISCLASSIFIED AND ASSIGNED BIOTOPE(S)							
		Riffle	Riffle/Run Trans	Run	Trickle Run	Pool/Run Trans	Pool	BackW	StandW
Riffle	64.6	X	0.2	33.1	0.5	0	1.7	0	0
Riffle/Run Trans	1.6	37.1	X	58.1	0.8	0	2.4	0	0
Run	85.1	7.9	0	X	0.7	0.1	6.3	0	0
Trickle Run	9.1	0	9.1	18.2	X	0	63.6	0	0
Pool/Run Trans	1.2	1.2	0	53.5	2.3	X	41.9	0	0
Pool	64.6	0.3	0	34.5	0.6	0	X	0	0
Backw	0	0	0	7.1	0	0	92.9	X	0
Stand	0	0	0	0	0	0	100	0	X
Total	**64.7**								

Table 6.13 Proportion of cases where flow turbulence was recorded (%) or absent (none) at average (0.6V) and near-bed (NBV) velocities, and where hydraulic refuges were created by large bed elements upstream of field sampling points, for all hydraulic biotopes.

BIOTOPE	TURBULENCE AT 0.6V (%)	TURBULENCE AT NBV (%)	HYDRAULIC REFUGE (%)
Riffle	23.7	22.4	9.0
Riffle/run transition	8.1	6.5	7.3
Run	13.6	11.2	16.3
Trickle run	none	none	none
Pool/run transition	none	none	22.1
Pool	none	none	6.0
Backwater	none	none	none
Standing water	none	none	none

Discriminant analysis using only derived hydraulic variables, but based on the aggregate data set and all biotopes, confirmed Fr as the most powerful single, derived hydraulic variable in discriminating across biotopes (Partial Wilks' Lambda = 0.71, F = 110.272), with the first discriminant function explaining more than 91% of observed variability. Classification of biotopes was correspondingly elevated at 92% for runs, though below the predetermined threshold at 61% for riffles. Moreover, Fr alone was less able to delineate

lower energy environments such as pools and pool/run transitional patches as separate biotopes from runs, in particular, with fewer than 22% of pool cases correctly classified. Overall classification ability was weak at around 58%.

Analysis of the three biotopes from which invertebrates were sampled (Table 6.14) revealed essentially the same results as the analysis based on all biotopes, although the relative importance of Fr diminished compared with substratum size. In addition, although total classification success was increased through removing the variability potentially generated by other biotopes, the individual percentages of cases correctly classified remained similar, as did the most common misclassifications (Table 6.15).

Table 6.14 Results of forward stepwise discriminant analysis for classification of the three main hydraulic biotopes based on an aggregate data set.

	MODEL		
***n* = 1689**	**Wilks' Lambda = 0.444**	**Approx. F (18, 3356) = 93.456**	***P* < 0.000**
Model variables (*n* = 9)	**Partial Wilks' Lambda**	**F-remove (2, 1678)**	**p-level**
Depth	0.951	43.612	0.000
$SUBd_{50}$	0.966	29.252	0.000
NBV	0.972	24.288	0.000
Re	0.988	9.982	0.000
Fr	0.990	8.673	0.000
TI	0.995	3.952	0.019
R_{rel}	0.996	3.249	0.039
RE	0.998	1.499	0.224
VD_{ratio}	0.999	1.003	0.367

Table 6.15 Classification matrix for the discriminant analysis summarised in Table 6.14.

BIOTOPE	PERCENT CORRECTLY CLASSIFIED	PERCENT OF CASES MISCLASSIFIED AND ASSIGNED BIOTOPE(S)		
		Riffle	Run	Pool
Riffle	64.6	X	33.9	1.5
Run	85.8	7.9	X	6.3
Pool	63.7	0.3	36.0	X
Total	**74.0**			

Discharge dependency of hydraulic biotopes, with specific reference to extreme low flows

The extent to which the biotope types from which invertebrates were sampled (i.e. riffles, runs and pools) maintained their discreteness as habitat units across the full low flow range was addressed through comparative discriminant analysis of biotope patches from three separate discharge groups (see Section 3.4.4 for group derivations): (1) the higher end of the range of low flows (commonly associated with early summer

or early autumn, but still part of the river's low flow regime, 'high'); (2) the natural range of discharges experienced, including low flows at the peak of the dry season ('natl'); and (3) the range of discharges representing manipulated low flows below historical minima ('extl'). Biotope hydraulic character for the aggregate data set representing the full suite of discharges encountered ('aggr') is summarised in Appendix 6.3. Although the emphasis here was on the main biotopes, analyses of all eight biotopes yielded similarly poor classification of transitional and other biotopes to that of the aggregate analysis (see above), for all three discharge groups.

Classification of hydraulic biotopes under conditions of elevated low flows was most robust when both core and derived variables were included in the discriminant analysis, based on a six-variable model (n = 530, Wilks' Lambda = 0.504, F = 35.488, P < 0.0001; Table 6.16). No single hydraulic variable dominated overall, though Fr remained the best variable. The use of solely derived variables or consideration of all biotopes produced models of marginally poorer discriminatory capacity, but with Fr still the most influential variable. From canonical analysis, it was apparent that only two discriminant functions were required to account for all explained variance. The discriminatory power of the first function (Eigenvalue = 0.814, χ^2 = 358.867, Wilks' Lambda = 0.504, DF = 12, P = 0.000), largely a function of Fr (standardised coefficient (Std. Coeff.) = -0.556) and NBV (Std. Coeff. = -0.504), accounted for 90% of the observed variance. The second function (Eigenvalue = 0.093, χ^2 = 46.644, Wilks' Lambda = 0.915, DF = 5, P = 0.000) contributed the remaining variance through the hydraulic combination of depth (0.653) and relative exposure (RE, 0.569). Comparison of canonical variable means showed a great divergence between pools and riffles, with the former exhibiting very low Fr values, despite greater magnitude discharges, compared with consistently high figures for riffles. Along the second axis of discrimination, pools especially, and riffles were highlighted by their high relative exposure (/low relative submergence), contrasted with depth-driven, lower values in runs. Classification using the 'high' data set, was more successful overall than for the aggregate data set (Table 6.17 cf. Table 6.12), but yielded similarly high degrees of success for the main biotopes with few outliers.

Across the natural set of low flows characteristic of the dry season ('natl'), discrimination among the main biotopes was best when both core and derived variables were incorporated in the model (n = 1007, Wilks' Lambda = 0.409, F = 62.286, P < 0.0001; Table 6.18). Froude number exerted considerably less influence in the model than depth. The first two discriminant functions were sufficiently powerful in combination to account for all explained variance, according to canonical analysis results. The first function, which accounted for 79% of observed variance (Eigenvalue = 0.951, χ^2 = 892.988, Wilks' Lambda = 0.409, DF = 18, P = 0.000), was weighted most by NBV (Std. Coeff. = -0.972), with VD_{ratio} playing a lesser role in discrimination (Std. Coeff. = -0.488). The remaining explained variance was largely accounted for by depth (-1.069), with weaker contributions by Re and $SUBd_{50}$ (second function: Eigenvalue = 0.252, χ^2 = 224.628, Wilks' Lambda = 0.799, DF = 8, P = 0.000). Root means of canonical variables firstly indicated distinct discrimination between the extremes in NBV and VD_{ratio} for pools and riffles - runs remained intermediate in

hydraulic character. Pools exhibited near-to-zero NBV and mean column velocities, coupled with lower ratios between 0.6V and depth at low discharges than the other two biotopes. Further discrimination between pools and other biotopes was on the basis of a decline in depths in the former type, coupled with an increase in laminar flow and the presence of fine bed material.

Table 6.16 Results of forward stepwise discriminant analysis for classification of the main hydraulic biotopes at naturally higher low flows ('high' data set).

	MODEL		
***n* = 530**	**Wilks' Lambda = 0.504**	**Approx. F (12, 1044) = 35.488**	***P* < 0.000**
Model variables (*n* = 6)	**Partial Wilks' Lambda**	**F-remove (2, 522)**	**p-level**
Fr	0.956	11.981	0.000
NBV	0.961	10.681	0.000
Depth	0.961	10.659	0.000
RE	0.980	5.462	0.004
$SUBd_{50}$	0.983	4.539	0.011
R_{rel}	0.993	1.870	0.155

Table 6.17 Biotope classification matrix for naturally higher low flows.

BIOTOPE	PERCENT CORRECTLY CLASSIFIED	PERCENT OF CASES MISCLASSIFIED AND ASSIGNED BIOTOPE(S)		
		Riffle	Run	Pool
Riffle	65.3	X	33.8	0.9
Run	81.9	12.6	X	5.6
Pool	64.7	1.0	34.3	X
Total	**71.9**			

Biotopes remained robust in character at natural lowest flows midsummer with marginally improved classification results for only runs (Table 6.19), when results were compared with the 'high' discharge matrix (Table 6.17). However, a fair number of riffle and pool cases remained misclassified as runs. With the use of only derived hydraulic indices, discrimination was weaker and especially poor for pools (a high number were classified as runs, with Fr as the key variable).

Of all discharge groups examined, by far the most distinctive results were obtained with discriminant analysis of extreme low flows ('extl') and based solely on derived hydraulic variables. The resultant model exhibited the strongest discriminatory power of all models, with only four variables (n = 152, Wilks' Lambda = 0.359, F = 24.404, P << 0.001; Table 6.20). Froude number contributed the most in discriminatory power. The first discriminant function was sufficiently powerful to explain 97% of the variance (Eigenvalue = 1.652, χ^2 = 151.034, Wilks' Lambda = 0.359, DF = 8, P = 0.000). It was heavily

weighted by Fr (Std. Coeff. = -1.225), with Re, Relative roughness (R_{rel}, the principal variable along the second axis) and VD_{ratio} playing lesser roles in discrimination (range in Std. Coeff.: -0.252 to 0.386; see below for further discussion). Based on the root means of canonical variables, riffles were clearly distinguished from the other two biotopes by elevated R_{rel}, Fr and VD_{ratio} figures, coupled with a decrease in Re, when discharges fell below historical minima.

Table 6.18 Results of forward stepwise discriminant analysis for classification of the main hydraulic biotopes at natural, midsummer low flows ('natl' data set).

MODEL			
***n* = 1007**	**Wilks' Lambda = 0.409**	**Approx. F (18, 1992) = 62.286**	***P* < 0.000**
Model variables (*n* = 9)	**Partial Wilks' Lambda**	**F-remove (2, 996)**	**p-level**
Depth	0.888	62.711	0.000
$SUBd_{50}$	0.952	25.149	0.000
NBV	0.986	6.992	0.001
TI	0.991	4.759	0.009
R_{rel}	0.991	4.402	0.012
Re	0.994	3.208	0.041
VD_{ratio}	0.994	2.756	0.064
VS	0.995	2.275	0.103
Fr	0.999	0.251	0.778

Table 6.19 Biotope classification matrix for the natural, dry-season discharge regime.

BIOTOPE	PERCENT CORRECTLY CLASSIFIED	PERCENT OF CASES MISCLASSIFIED AND ASSIGNED BIOTOPE(S)		
		Riffle	Run	Pool
Riffle	65.8	X	31.0	3.2
Run	87.2	7.0	X	5.8
Pool	64.3	0	35.7	X
Total	**75.8**			

Corresponding with model results, biotope classification was most robust for the 'extl' group, with an overall success of 86% (Table 6.21). More than 70% of cases for all biotopes were correctly classified, reaching 98% for pools (typically poorly classified in the original aggregate analysis). A moderate degree of misclassification remained for riffles in particular, many of which were assigned to runs at much reduced discharges. Furthermore, there was found to be an increased risk, though small, of misclassifying runs as pools at very low discharges.

In a similar analysis using both core and derived indices, R_{rel} was identified as the key discriminator, though FR, 0.6V, $SUBd_{50}$ and turbulence index (TI) also contributed to biotope differentiation. An analysis

including transitional biotopes demonstrated that at extremely reduced discharges, pool/run transitions were most similar to pools (rather than runs - as found when all discharge data were aggregated), while riffle/run transitions could not readily be distinguished from runs. It was not possible to similarly compare the character of the other biotopes recorded in the field, due to small numbers of observations for the majority of them.

Table 6.20 Results of forward stepwise discriminant analysis for classification of the main hydraulic biotopes at extreme low flows ('extl' group), using derived hydraulic indices.

MODEL			
n = 152	Wilks' Lambda = 0.359	Approx. F (8, 292) = 24.404	*P* < 0.000
Model variables (*n* = 4)	**Partial Wilks' Lambda**	**F-remove (2, 146)**	**p-level**
Fr	0.847	13.217	0.000
R_{rel}	0.953	3.603	0.030
Re	0.976	1.766	0.175
VD_{ratio}	0.985	1.107	0.333

Table 6.21 Biotope classification matrix for extreme low flows.

BIOTOPE	PERCENT CORRECTLY CLASSIFIED	PERCENT OF CASES MISCLASSIFIED AND ASSIGNED BIOTOPE(S)		
		Riffle	Run	Pool
Riffle	74.3	X	25.7	0
Run	81.5	4.6	X	13.8
Pool	98.1	0	1.9	X
Total	**85.5**			

These findings suggested that the general hydraulic character of biotopes was more clearly defined at extreme low flows than under the natural low flow regime. Changes in character at extreme discharges was explored through comparative statistical analysis of biotope hydraulics, with the main emphasis placed on Fr as the best discriminatory variable across biotopes with changes in low flow regime.

Analysis of variance comparing Fr values across hydraulic biotopes (Figure 6.22), irrespective of discharge group, indicated highly significant inter-biotope differences (H (4, 3798) = 2459.838, *P* = 0.000) (means in Appendix 6.3). However, pool and pool/run transitional biotopes were the most alike of all biotope pairs examined.

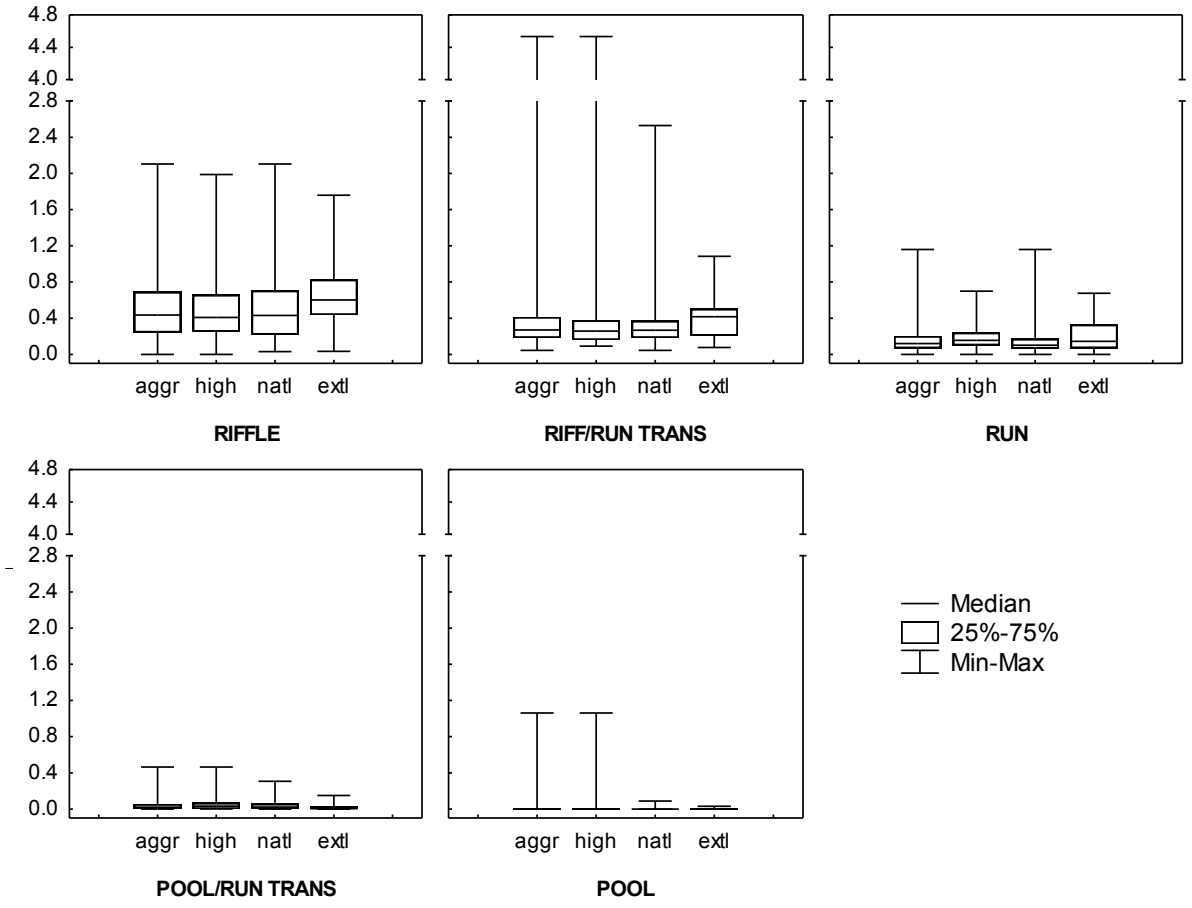


Figure 6.22 Froude number distributions for individual hydraulic biotopes, across four discharge groups. Aggr - aggregate; high - higher low flows; natl - natural low flows; extl - extreme low flows. Note the scale break to account for high variability for the riffle/run transitional biotope.

When comparing biotopes, the greatest discharge-linked changes in Fr number were evident for runs (H (3, 1526) = 39.377, $P = 0.000$), with the most significant difference recorded for the 'high' discharge group versus the 'natl' and 'aggr' groups. This variation was probably largely due to inadequate recognition of broad categories of hydraulic condition within this biotope type (Section 6.7). Although there were no highly significant differences in riffle Fr values across discharge groups, the 'extl' group diverged from all other groups, showing significantly higher values (Figure 6.22). For pools, the only significant difference observed was due to increased variability at the higher end of the flow spectrum, as compared with negligible variation at extreme low flows where Fr values were very close to or at zero (Table 6.22). Pool/runs and riffle/runs retained their intrinsic character, in terms of Fr values, irrespective of discharge. The 'extl' group differed most from the other discharge groups for both transitional biotopes, with decreased variability in Fr numbers (Figure 6.22).

Table 6.22 **Results of Kruskal-Wallis ANOVA by ranks for comparisons of Froude numbers among the four discharge groups, for the main hydraulic biotopes and transitional biotopes.** Discharge groups: aggr – aggregate; high – higher low flows; natl – natural low flows; extl – extreme low flows. Mann-Whitney U test results for within-biotope, *post hoc* comparisons of discharge groups are given in the final column. DF – degrees of freedom; *n* – no. of observations. *NS* (not significant); * ($0.01 < P \leq 0.05$); ** ($0.001 < P \leq 0.01$); *** ($P \leq 0.001$).

HYDRAULIC BIOTOPE	DF	*n*	*H*	*P*	WITHIN-BIOTOPE COMPARISONS AMONG DISCHARGE GROUPS
Riffle	3	1180	9.158	* 0.027	NS Aggr vs. High (U = 61 578.0, *P* = 0.665) NS Aggr vs. Natl (U = 99 189.0, *P* = 0.668) ** Aggr vs. Extl (U = 7367.0, *P* = 0.004) NS High vs. Natl (U = 36 381.5, *P* = 0.982) ** High vs. Extl (U = 2512.0, *P* = 0.002) ** Natl vs. Extl (U = 4242.5, *P* = 0.005)
Riff/Run Trans	3	248	2.475	NS 0.480	No significant differences
Run	3	1526	39.377	*** 0.000	*** Aggr vs. High (U = 66 672.5, *P* = 0.000) ** Aggr vs. Natl (U = 166 034.5, *P* = 0.003) NS Aggr vs. Extl (U = 21 917.5, *P* = 0.120) *** High vs. Natl (U = 36 777.0, *P* = 0.000) NS High vs. Extl (U = 6783.0, *P* = 0.721) ** Natl vs. Extl (U = 12 613.0, *P* = 0.010)
Pool/Run Trans	3	172	2.825	NS 0.419	No significant differences
Pool	3	672	11.984	** 0.007	NS Aggr vs. High (U = 15 223.5, *P* = 0.088) NS Aggr vs. Natl (U = 28 206.5, *P* = 0.145) NS Aggr vs. Extl (U = 8279.0, *P* = 0.544) ** High vs. Natl (U = 7547.5, *P* = 0.009) NS High vs. Extl (U = 2474.0, *P* = 0.496) NS Natl vs. Extl (U = 4097.0, *P* = 0.140)

Based on the results for Fr, statistical comparison of biotope hydraulics for the remaining indices was performed for only extreme ('extl') and natural ('natl') low flows, for the three main biotopes, specifically to identify the extent to which there were biotope-specific, hydraulic responses to flow reduction. Exclusion of the higher range of natural discharge ('high') minimised the effects of discharges outside of those of the dry season proper. The results (Table 6.23) revealed that the greater success in discriminating biotopes at extreme than at natural low flows was not simply a function of biotopes experiencing the lower limits of ranges in hydraulic variables or decreased variability in the former instance. Rather, it was due to multiple and complex shifts in hydraulic character with severe decreases in discharge.

Effects of extreme discharge reduction were most pronounced for runs in terms of the number of hydraulic indices exhibiting a significant or highly significant response (nine). Declines were experienced in depth

(0.20 m cf. 0.10 m), and to a lesser extent particle size (suggesting localised accumulation of gravels and fines). Increases in the ratio of velocity to depth (1.47 s^{-1} cf. 2.88 s^{-1}), the relative protrusion of bed elements with shallower water (a decrease in RE), and the prevalence of smooth flow (decreased Re and R_{rel} values) were also striking. Although riffles showed significant changes in five hydraulic indices with the shift from natural to extreme low discharges, the only two highly significant responses were a decrease in water depth (0.12 m cf. 0.07 m), and an increase in VD_{ratio} from a mean of 6.63 s^{-1} to a very high 11.53 s^{-1} (Table 6.23). Pools, in contrast with the other biotopes, basically retained their hydraulic character with flow diversion, though significant decreases in depth corresponded with increases in both bed exposure and flow roughness (Table 6.23).

Table 6.23 Pairwise comparisons of hydraulic indices for natural low flow versus extreme low flow groups, for the main biotopes sampled. Highly significant differences based on Mann-Whitney U tests are shaded ($P \leq 0.001$). The direction of change in each index with discharge reduction from natural, based on mean values, is shown as an increase (+) or decrease (-) ('none' represents no change). Numbers of observations are indicated under each biotope for 'natl' and 'extl' discharge groups, respectively.

HYDRAULIC INDEX	RIFFLE (342, 35)			RUN (483, 65)			POOL (182, 52)		
	+ or -	U	*P*	+ or -	U	*P*	+ or -	U	*P*
Depth	-	3756.5	0.000	-	7062.0	0.000	-	3778.0	0.027
Mean column velocity	+	5341.0	0.294	none	15 680.0	0.988	-	4090.5	0.136
Near-bed velocity	+	5082.0	0.141	+	14 993.5	0.557	-	4226.5	0.240
Substratum d_{50}	none	5269.0	0.244	-	11 703.5	0.001	none	4391.5	0.429
Velocity: depth ratio	+	3891.5	0.001	+	10 783.0	0.000	-	4095.0	0.139
Velocity shelter	-	5961.0	0.969	-	12 722.5	0.013	+	4613.0	0.782
Froude number	+	4242.5	0.005	+	12 613.0	0.010	-	4097.0	0.140
Relative exposure	-	4714.0	0.038	-	11 856.5	0.001	-	3788.5	0.028
Turbulence index	-	5052.0	0.129	-	12 349.5	0.005	+	4074.0	0.126
Reynolds number	-	4541.5	0.019	-	9405.0	0.000	-	4064.0	0.121
Relative roughness	+	4714.0	0.038	-	11 865.5	0.001	+	3786.5	0.028
Shear velocity	+	4717.0	0.039	+	13 723.5	0.100	-	3971.0	0.096
Roughness Reynolds number	+	5600.0	0.531	-	14 910.0	0.511	-	3969.0	0.095

6.4.3 Differences in the integrity and hydraulic character of biotopes across sites

Based on the results presented in Table 6.24, hydraulic biotopes were sufficiently rigorously classified at all sites using a combination of core and derived hydraulic indices. The models capable of strongest and weakest discrimination among biotopes, respectively, were for the Elands (Wilks' Lambda = 0.360, 80% total classification success) and Riviersonderend sites (Wilks' Lambda = 0.511; 70% total classification success). Clearly though, the hydraulic variables most responsible for the discrimination among biotopes differed according to site. Moreover, Fr, though still influential, was less powerful a discriminator than depth, NBV and TI (Table 6.24). Although individual biotopes were found to be robust in type, in general,

riffles were commonly the most poorly classified. The exception was the Riviersonderend River, where pools lacked adequate integrity (48% cf. the designated 65% threshold). Results for discriminant analysis of all biotopes and analysis based on only the derived hydraulic indices were highly similar to those of the preliminary aggregate analysis above.

Of special interest in terms of the ecological relevance of biotopes to invertebrates (Chapter 7) was the degree to which the main biotopes visually assigned in the field retained their integrity (type) and hydraulic character at individual sites with extreme discharge reduction ('extl' Q group). As a control site, the Elands demonstrated the comparative success in hydraulics-based biotope classification under conditions of natural low flows (see Table 6.24) - the entire data set for this site fell within the 'natl' Q group. Results conclusively demonstrated that biotopes not only maintained their basic type at extreme low flows at individual sites, but as for discriminant analysis based on discharge groups, were more discrete than when cases were pooled (Table 6.25). The power of the discriminant models for the experimental sites was high, and greatest for the Molenaars impact location (Wilks' Lambda = 0.187). It exceeded the results at extreme low flows for all sites in combination (Table 6.20). All biotopes at all sites could be considered highly discrete in character, with classification successes ranging from 71% for pools in the Molenaars impact location (marginal slackwaters, and deeper, partially channel-spanning pools) to 100% for Du Toits pools (predominantly shallow, marginal slackwaters). The hydraulic indices contributing most to the separation of biotopes varied among sites, however, with only Re and TI influential across all reaches (and the control site) (Tables 6.24 and 6.25). Notably, Fr again showed a diminished ability to differentiate biotopes at site scale, as compared with across discharge groups. At all experimental sites, the majority of variance was explained by the first two discriminant functions, with greatest separation along the first axis (93% of variance) achieved in the Molenaars reach (a function of Re and mean column velocity).

Given the above disparities in the extent to which different hydraulic indices were responsible for biotope character across the reaches, at natural and abnormal low flows, an analysis of the variation in hydraulic variables among sites was undertaken. As extreme low ('extl') and elevated ('high') discharges were known to influence hydraulic indices, only the natural low flow data set ('natl') was used. The results of Kruskal-Wallis ANOVA, presented in Table 6.26 (with corresponding site means indicated), yielded significant inter-site differences for all four core variables, as well as the complex indices VD_{ratio} and Fr.

Table 6.24 **Results of forward stepwise discriminant analysis for site-specific classification of the main hydraulic biotopes (aggregate data set combining all discharge groups).** (1) Model. (2) Classification matrix. Both core and derived hydraulic indices were included. Model variables are presented in approximate order of decreasing discriminatory power. Key variables, on the basis of partial Wilk's Lambda values and standardized coefficients for significant discriminant functions, are shaded.

SITE	(1) MODEL												
	n	Wilks' Lambda	Approx. F	*P*	Variables								
EL	492	0.360	(12, 968) = 53.822	< 0.000	Depth	$SUBd_{50}$	Fr	Re	NBV	TI			
MO	412	0.379	(16, 804) = 31.369	< 0.000	TI	Depth	RE	Re	$SUBd_{50}$	NBV	0.6V	Fr	
DU	365	0.369	(14, 712) = 32.877	< 0.000	Depth	Re	Fr	TI	R_{rel}	NBV	VD_{ratio}		
RI	420	0.511	(12, 824) = 27.410	< 0.000	NBV	$SUBd_{50}$	Fr	RE	R_{rel}	Depth			

(2) CLASSIFICATION MATRIX

Percent correctly classified

	Riffle	Run	Pool	Total
EL	68.4	91.3	65.8	80.3
MO	66.0	87.2	81.3	78.2
DU	62.7	76.5	79.8	72.9
RI	67.1	85.0	47.7	70.2

Table 6.25 Results of forward stepwise discriminant analysis for classification of the main hydraulic biotopes at the experimental sites, at extreme low flows ('extl' Q group). (1) Model. (2) Classification matrix. Both core and derived hydraulic indices were included.

SITE	(1) MODEL									
	n	Wilks' Lambda	Approx. F	*P*	Variables					
MO	58	0.187	(12, 100) = 10.935	< 0.000	$SUBd_{50}$	0.6V	TI	Depth	Re	Fr
DU	47	0.268	(8, 82) = 9.565	< 0.000	Fr	VD_{ratio}	Re	TI		
RI	47	0.271	(12, 78) = 5.986	< 0.000	TI	NBV	$SUBd_{50}$	R_{rel}	VD_{ratio}	Re

(2) CLASSIFICATION MATRIX

Percent correctly classified

	Riffle	Run	Pool	Total
MO	89.5	94.4	71.4	84.5
DU	85.7	75.0	100.0	85.1
RI	88.9	87.0	80.0	85.1

Table 6.26 Results of Kruskal-Wallis ANOVA and corresponding mean values for select hydraulic indices across the sites at natural low flows ('natl' discharge group). (H: 3, *N* = 1165). *** *P* ≤ 0.001.

			VARIABLE MEANS PER SITE			
HYDRAULIC VARIABLE	**H**	***P***	**EL**	**MO**	**DU**	**RI**
Depth (m)	60.050	***0.000	0.169	0.157	0.101	0.146
Mean column velocity (m s^{-1})	20.976	***0.000	0.189	0.276	0.247	0.225
Near-bed velocity (m s^{-1})	18.729	***0.000	0.166	0.242	0.222	0.203
Substratum d_{50} (m)	58.971	***0.000	0.199	0.212	0.116	0.173
Velocity: depth ratio (s^{-1})	23.335	***0.000	2.405	3.669	4.290	3.298
Velocity shelter (m s^{-1})	3.823	0.281	0.023	0.034	0.026	0.023
Froude number	23.226	***0.000	0.188	0.273	0.284	0.249
Relative exposure	3.127	0.372	1.393	1.184	1.980	1.492
Turbulence index (m s^{-1})	6.319	0.097	0.229	0.350	0.506	0.284
Reynolds number	11.345	0.010	29 123.6	46 967.8	26 521.9	27 826.0
Relative roughness	3.120	0.374	3.425	4.469	2.983	3.142

6.5 REACH-SCALE BIOTOPE PATCH DYNAMICS AND DIVERSITY IN RELATION TO DISCHARGE

6.5.1 Biotope patch dynamics with changing discharge

The degree of reach-scale change in total wetted surface area is illustrated in Figure 6.23 for select site locations, across the broadest possible range of low flows. The Molenaars site had the greatest surface area available as physical habitat of all sites (a maximum of 969.9 m^2 in May) commensurate with its size, while the lowest wetted area of all sites was recorded for the Du Toits, especially at extreme low flows (333.0 m^2 in February, impact location). Over the dry season, the approximate percentage decreases in reach wetted area were as follows: 9% (EL - control); 16% (MO); 21% (RI); and 32 % (DU). In contrast with the other experimental sites, however, the Riviersonderend showed limited evidence of a progressive decrease in wetted surface area with decreasing discharge (Figure 6.23).

Even based on a limited data set (Section 3.4.1), the river sites exhibited differences in the proportions of biotope types existing under natural (as well as manipulated) flows, but with certain biotopes, such as trickle runs and standing waters, routinely present as only small proportions of total wetted area (Table 6.27). The often fairly wide ranges in biotope proportions observed over the study period in a single reach further underscored the dynamic nature of biotope patches. Runs were characteristically dominant at all sites at all discharges, although in the Riviersonderend reach they alternated with pools in terms of highest representation. While differences in the proportions of various biotope types over the study were low (below 22%) for the Elands control site, at the other sites, in several instances directly as a result of large-scale reduction in discharge, ranges exceeded 50% (e.g. for runs at the Du Toits and Riviersonderend sites, as well as for pools at the latter site).

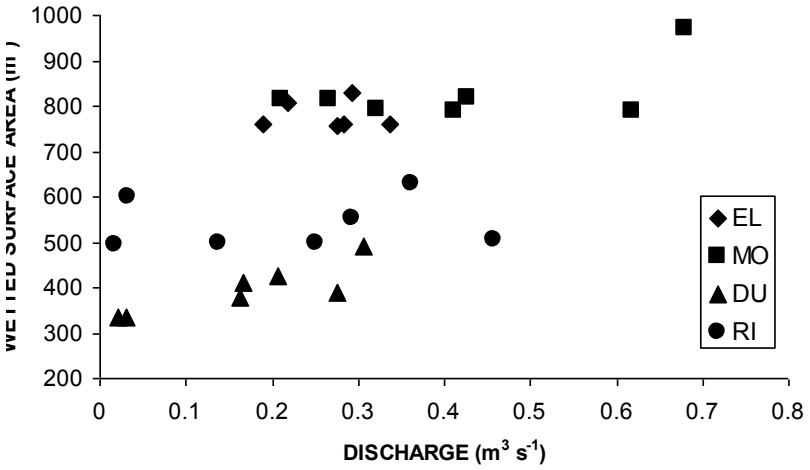


Figure 6.23 Mapped wetted surface areas (m^2) in relation to discharge at the sites. Surface areas were calculated for a unit reach length of 60 m, with data from a combination of site control and impact locations represented.

Table 6.27 Ranges in the percentages that different biotope types represented at each site over the study period. Ranges are based on a standard 60 m location length, with data from both locations and all experimental phases pooled. Minima and maxima per biotope type are indicated in italics and bold, respectively.

SITE	ELANDS		MOLENAARS		DU TOITS		RIVIERSONDEREND	
BIOTOPE (%)	Min	Max	Min	Max	Min	Max	Min	Max
Riffle	5.1	27.4	17.7	32.0	*1.3*	**41.2**	3.8	28.8
Riffle/run transition	6.7	25.1	4.6	**28.7**	5.2	26.3	*2.3*	16.8
Run	41.1	63.3	25.3	55.4	22.5	**76.0**	*6.0*	61.8
Trickle run	0.1	0.3	0.2	0.9	*0.0*	0.3	*0.0*	**1.8**
Pool/run transition	5.4	18.6	7.6	15.3	*0.0*	12.3	1.9	**23.6**
Pool	3.3	7.3	*2.9*	12.7	3.3	18.8	7.7	**61.7**
Stand	0.1	1.0	*0.0*	1.3	0.1	1.1	0.5	**10.9**

Based on the percentages of wetted surface area represented by individual biotope types (e.g. as per Figure 3.6) across the range of natural to abnormally low discharges examined, generalised best-fit relationships between the proportions of different biotopes and discharge were determined (Table 6.28).

A general, typically non-linear, decrease in the proportions of higher energy biotopes with decreasing discharge was observed, especially evident for riffles (R^2 = 0.45). This trend was coupled with a greater surface area under low energy pool/run transitions, pools and standing waters. Only one simple linear relationship was found, for trickle runs. Separate examination of the lowest energy biotopes, combined as 'pool' in Table 6.28, showed that the proportions of wetted surface area represented by pools within the main channel, along the channel margins, or isolated from the flowing channel, all increased with discharge

reduction (Figure 6.24). There was increased isolation of pools, with the number that were entirely isolated (i.e. no surface contact with flowing water) highest at extreme low flows. At discharges above Q_{inst}: Q_{50} = 0.2, the contribution of this pool type to reach wetted area was negligible.

Table 6.28 Relationships between reach-scale biotope proportions and discharge. Equations represent the best fit of a linear, logarithmic (natural), power or exponential function (R^2 = coefficient of determination; n = 27). The 'pool' category combines several types: marginal, midstream and isolated pools, as well as occasional backwaters.

BIOTOPE TYPE	TREND WITH ↓ Q	EQUATION	R^2
Riffle	↓	$y = 34.338x^{0.650}$	0.445
Riffle/run transition	↓	$y = 21.174x^{0.391}$	0.221
Run	↓	$y = 44.557x^{0.173}$	0.053
Trickle run	↓	$y = 1.046x - 0.008$	0.260
Pool/run transition	↑	$y = -1.460\ln(x) + 8.209$	0.052
Pool	↑	$y = 4.181x^{-0.560}$	0.267
Standing water	↑	$y = -1.849\ln(x) - 1.151$	0.356

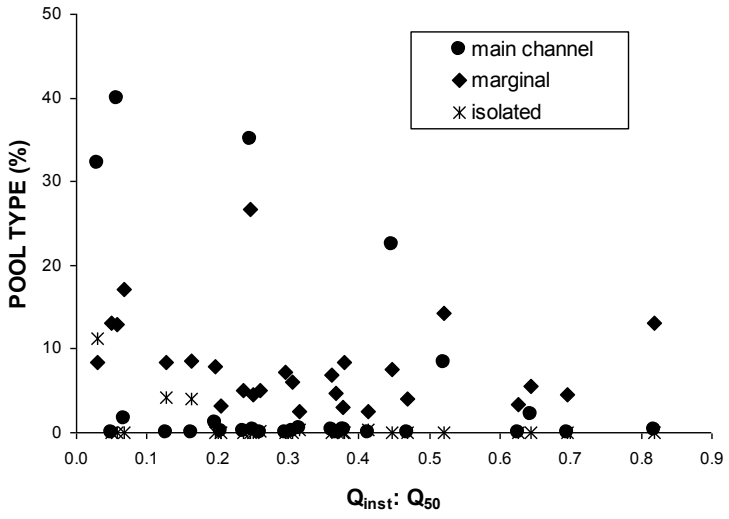


Figure 6.24 Generalised relationships between the proportions of different types of pools and discharge.

Results of site-specific assessments of the dynamics of the major biotopes with discharge are presented in Figure 6.25. Over the narrow range of discharges experienced at the control site, relationships between discharge and biotope patch proportions were relatively weakly developed (Figure 6.25a). Pools, and particularly runs, were in smaller proportions at lower discharges, while riffles increased.

At the Molenaars site (Figure 6.25b) relationships were the converse of those at the Elands and markedly stronger. Natural trends in biotope dynamics with discharge were reinforced with reduction to abnormal levels, with conclusive increases in areal representation by runs and pools (R^2 = 0.84 and 0.95, respectively), as well as in riffle/run transitions and standing waters. Isolated pools increased most of all pool types, from a recorded maximum under natural conditions of 0.4% to *c.* 4% at extremely low discharges. In contrast, riffle area was most reduced at lowest magnitude discharges. For the Du Toits reach, diametrically opposite trends from the control site also were observed for runs and riffles (Figure 6.25c). Riffle area declined dramatically in a linear manner (R^2 = 0.84) with discharge reduction to only 1% of reach wetted area (cf. approx. 10% at the peak of the dry season). Changes in run area with discharge diversion simply represented the extension of a moderate-strength natural trend. The distinctly non-linear, strong increase in dominance by pools with discharge reduction was most pronounced at extremely low discharges, especially for pools occurring along the river margins (8% naturally cf. 17% for the impact location, in Feb-Mar). Increases in the surface area occupied by riffle/run and pool/run transitional biotopes, as well as standing water patches, were also recorded in the impact phase, as compared with natural conditions.

The Riviersonderend showed a different trend from the other two experimental sites in that runs decreased in proportional representation with flow reduction. The difference might be explained by the natural high dominance by pools (due to bed topography) at many times during the dry season, as well as the clear increase in pool area relative to runs as discharges were reduced to below-natural magnitudes (Figure 6.25d). At severely reduced discharges, several natural pools along the river margins became entirely isolated (pers. obs.), representing 11% of wetted reach area (as compared with zero isolation under the natural hydrological regime). Though not as pronounced as within flow-impacted location of the Du Toits R., riffle area decreased exponentially (R^2 = 0.84) with decreasing discharge, with only 4% remaining when discharges dropped below historical minima (as compared with 10% under natural low flows, in Feb). Although transitional areas between riffles and runs were less apparent at extremely low discharges, an increase in pool/run patch area was observed (24% vs. 6% at natural low flows). Consistent with responses in standing waters at the other experimental sites, an increase in this biotope was recorded in the impact location in February to 11% of wetted area, compared with less than 1% under control conditions.

Sequences of biotope patch transformation with decreasing discharge

The transformation of individual patches representing the main biotopes, tracked across all reaches with fluctuations in discharge, highlighted several common sequences of change in patch type (Figure 6.26).

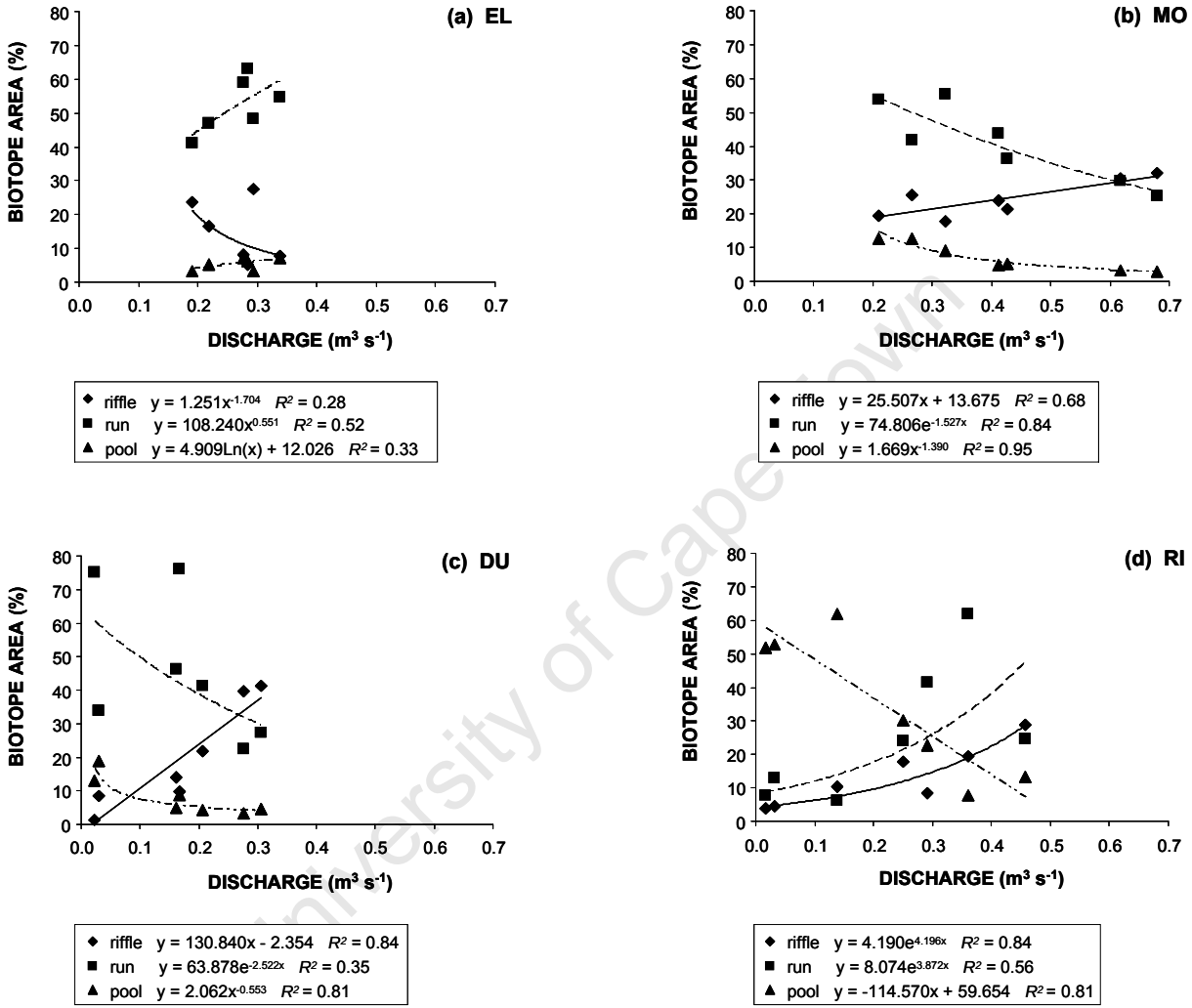


Figure 6.25 Site-specific relationships between reach proportions of the main biotopes and discharge. Best-fit trend lines are depicted for riffles (solid line), runs (dashed line) and pools (dot-dash line). Corresponding equations and coefficients of determination are provided below each plot. Axis scales are the same for all sites.

Multiple possibilities existed for the shift in patch type, and associated change in hydraulic characteristics, based on local bed topography, especially for riffles and runs. Pool patches, on the other hand, showed the least diverse behavioural responses to decreasing discharge, but with differing degrees of isolation a typical feature of this patch type (as also illustrated in Figure 6.24). Riffle patches typically transformed to run patches, in some instances with either increasing or decreasing discharge, and runs transformed into either riffles or pools, among other types. Pools were not recorded altering to riffles or the converse, highlighting the strong divergence between the hydraulic biotopes (and supporting previous results). Discharge reduction resulted in shifts from higher-energy to lower-energy patch types, often with quite different hydraulic character from the starting patch (based on earlier hydraulic analyses). For example, a riffle patch might transform, through riffle-run transition, then shallow run, to trickle run (Figure 6.26, riffle). Progressive dewatering led to areas of partially or wholly exposed streambed as a common endpoint; the same pattern was apparent above for transect-based analysis.

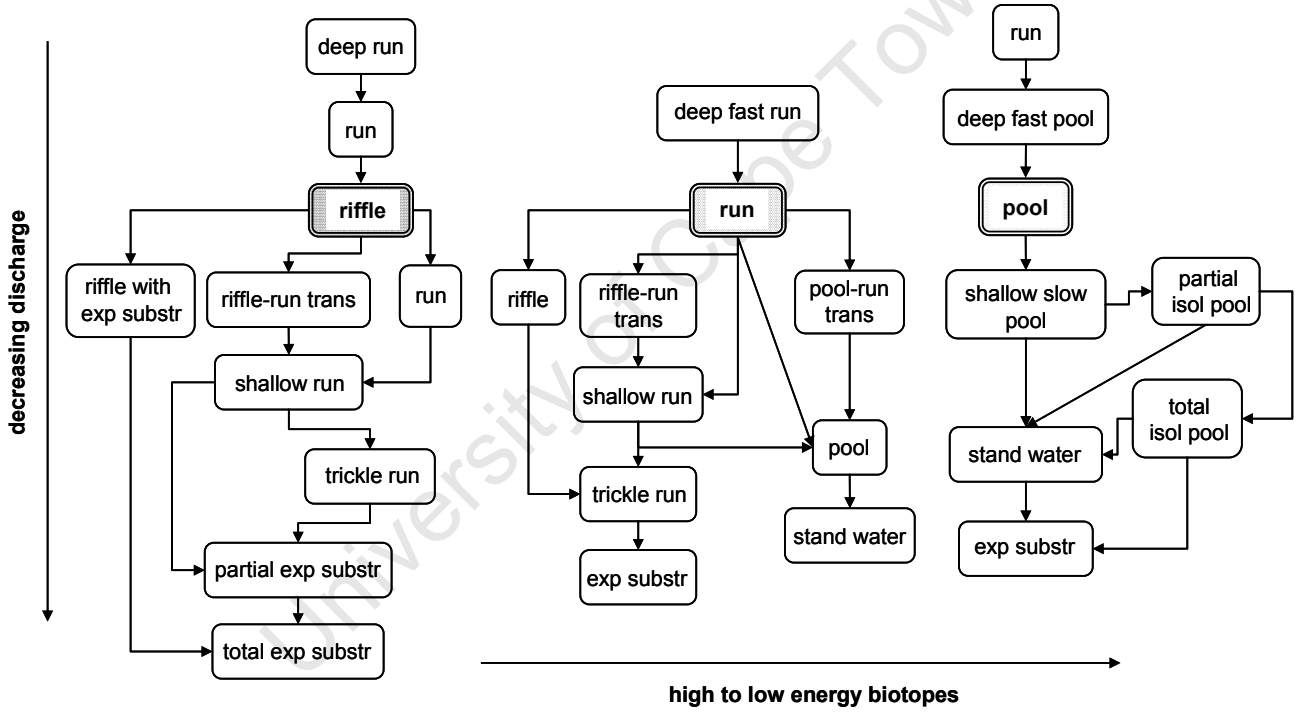


Figure 6.26 Generalised sequences of change in patch type for riffle, run and pool biotopes with decreasing discharge. Starting patch types are represented by the shaded double-bordered rectangles. Trans – transition; substr – substratum; exp – exposed; isol – isolated; stand – standing.

6.5.2 Biotope patch number and diversity at low flows

Assessment of the number of different patches, irrespective of biotope type, occurring per site location yielded the following mean (± SD) patch numbers per site: 52.2 ± 9.2 (Du Toits); 58.3 ± 12.7 (Elands); 61.0 ± 13.0 (Riviersonderend); and 66.9 ± 15.3 (Molenaars). Hence, spatially at the reach scale, potential patch heterogeneity (given the hydraulic variability of individual patches) was greatest for the Molenaars River and

lowest for the Du Toits site. Although in part a function of river size, patch number was clearly also related to the degree of variation in bed topography. Overall, in relation to discharge, there was a barely discernible positive trend in patch number (Figure 6.27; R^2 = 0.04). Relationships between discharge and site patch numbers were weak and inconsistent, except for the Elands R. where a distinctly positively linear relationship was found (Figure 6.27; R^2 = 0.66).

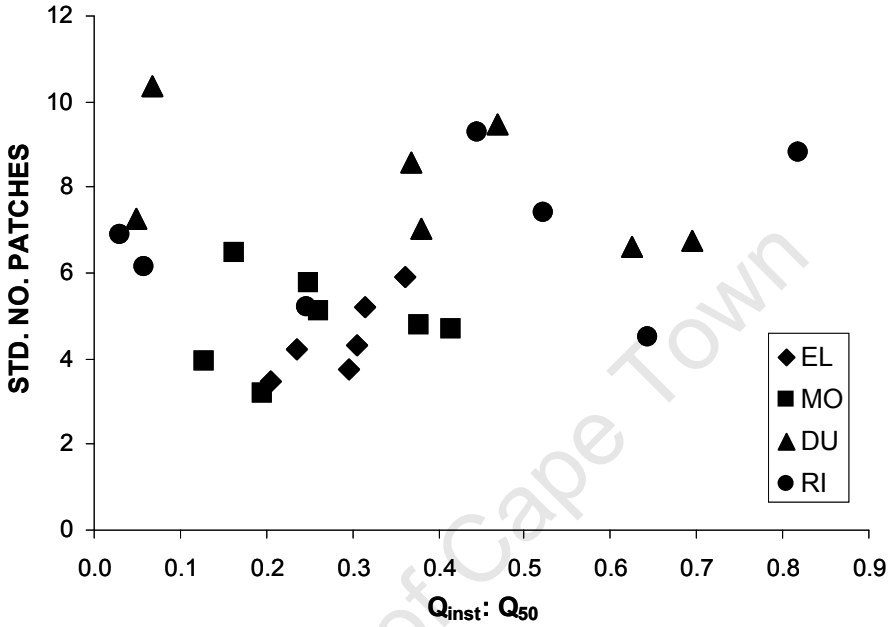


Figure 6.27 Generalised relationships between the number of biotope patches per location, standardised by mean channel width, and discharge.

Separate treatment of biotopes showed that across all sites, the number of pool patches in a reach typically was greater than those of riffles, and then runs, and increased non-linearly as discharge decreased (Figure 6.28). The converse response, though also weak, was shown for both riffles and runs (Figure 6.28). Non-standardised data showed the same trends, though relationships were better developed and linear for all biotopes. Ranges in numbers of patches across sites were: 6-21 for pools; 3-12 for riffles; and 1-11 for runs.

By site, changes in riffle, run, and pool patch number with discharge typically supported the generalized responses illustrated in Figure 6.28. The numbers of riffle and run patches at best showed weak relationships with discharge. The Molenaars site, which showed the best fit relationships of all sites, was an exception, showing moderate positive trends for runs and riffles (R^2 = 0.40 and 0.30, respectively). Notably, for all experimental sites, the number of pool patches increased with discharge reduction, counter to the natural trend.

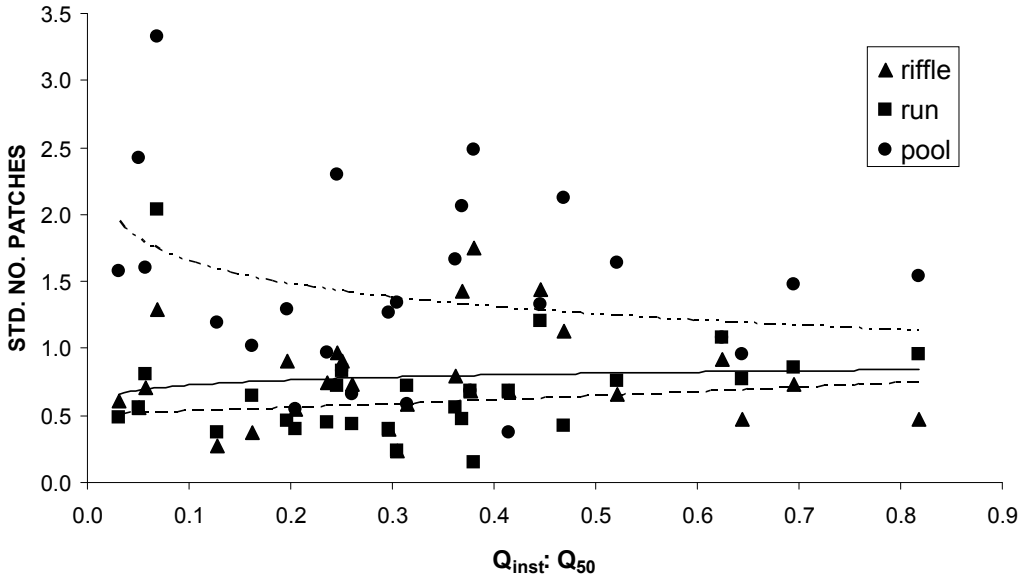


Figure 6.28 Generalised relationships between the numbers of pool, run and riffle patches per location and discharge. Variables were standardised to enable inter-site comparisons. Fitted trend lines are shown for pools (dot-dash line), runs (dashed line) and riffles (solid line).

Interrelationships between patch number and the size of the individual patches (i.e. areal extent) unquestionably contributed to the observed relationships, for instance, through coalescing of small patches (physically and/or in terms of hydraulic character), dissection of large patches, isolation of patches (e.g. through bed exposure) or increases in the extent of river bed under water at different discharges. Across all sites, pool patches tended to be small (mean patch size = 5.8 m^2) relative to run patches (55.1 m^2; reflecting their typical dominance within each reach), with riffle patches intermediate in surface area (17.0 m^2).

The average surface areas of patches for biotopes at individual sites showed a number of distinct trends in response to discharge fluctuations (Table 6.29). Typically, there was a marked decline in the mean areal extent of individual riffle patches with discharge reduction, particularly evident at the Du Toits and Riviersonderend sites where the range of discharges included extreme low flows (R^2 values of 0.83 and 0.89, respectively). In contrast, pool patch size increased on average with discharge reduction; the response was consistent and most dramatic at the Riviersonderend site (R^2 = 0.94). Runs showed no consistent response to discharge in terms of mean patch area, with a marked response (decrease) in mean area only in the Molenaars reach, with increasing discharge. It was noteworthy, however, that in a few cases areas of contiguous run formed an extremely large patch, interspersed with smaller patches representing other biotope types (e.g. single 312.3 m^2 patch, Du Toits control location, February).

Biotope diversity was relatively high at all sites given that six, or in most instances all seven biotope types (previously separated 'backwaters' were merged with other pools) were present on any sampling occasion.

Analysis of a standardised relationship between discharge and biotope diversity revealed only a weak, linear decrease in diversity with diminishing discharge (n = 27, y = 333.430x + 313.510, R^2 = 0.10).

Table 6.29 Site-specific relationships between mean patch size (m^2) and instantaneous discharge, for the main biotopes. Equations represent best-fit functions based on R^2 values (in parentheses).

SITE	EL	MO	DU	RI
Riffles	$y = 74.641e^{-6.164x}$ (0.335)	$y = -11.811\ln(x) + 15.068$ (0.172)	$y = 1.485e^{9.534x}$ (0.832)	$y = 3.004e^{4.962x}$ (0.885)
Runs	$y = 27.059\ln(x) + 115.430$ (0.018)	$y = 16.136x^{-1.008}$ (0.697)	$y = 55.296e^{-1.745x}$ (0.025)	$y = 7.542e^{2.952x}$ (0.397)
Pools	y = -5.496x + 4.667 (0.503)	$y = -2.616\ln(x) + 2.384$ (0.493)	$y = -0.709\ln(x) + 0.619$ (0.777)	y = -37.528x + 20.819 (0.936)

6.6 SUBSTRATUM AS A PRIMARY ELEMENT OF PHYSICAL HABITAT

6.6.1 Substratum composition within individual site reaches

Substratum composition, as an influential element of physical habitat affecting local hydraulics (Sections 6.3 and 6.4), was assessed for site reaches, including any natural variation between locations and among all biotope types. Temporal stability in bed substratum composition and orientation was as expected during the dry season, with no detectable changes over time at any of the sites or within biotopes (pers. obs.).

Based on data derived from both locations at each site (Figure 6.29), the Du Toits channel exhibited a markedly higher proportion of smaller sizes of substratum, and of more angular nature, than the other sites (all of which had predominantly sub-round to round particles). It was the only cobble-dominated site, with small cobble present in greatest proportions (26% of a total of 38% cobble), followed by large gravel (22%). Fines and gravels also were more prevalent in the same reach. The other three sites were dominated by boulders, especially small ones (20-34%), with cobble proportions above 20%. The Riviersonderend and Molenaars sites had far higher percentages of bedrock than the Elands site, at 20% and 16% respectively, while bedrock was absent from the Du Toits reach.

Despite evidence of variability in substratum composition between locations, overall substratum dominance by the main two or three size classes at a site tended to be maintained (Figure 6.29). Some degree of variability in substratum proportions was found for the following classes and sites: small boulder and large cobble (Elands); all boulder categories (Molenaars); sand, medium and large boulder (Du Toits); and small boulder and sand (Riviersonderend). As might be expected due to the large size of its individual elements, immobility and patchy location (in part due to rock in-falls from valley sides), inter-location variability in

bedrock proportions was high at all sites at which it occurred. Notably, invertebrates were collected from only a relatively narrow substratum range at individual sites, from large gravel to small cobble (Section 3.5.1).

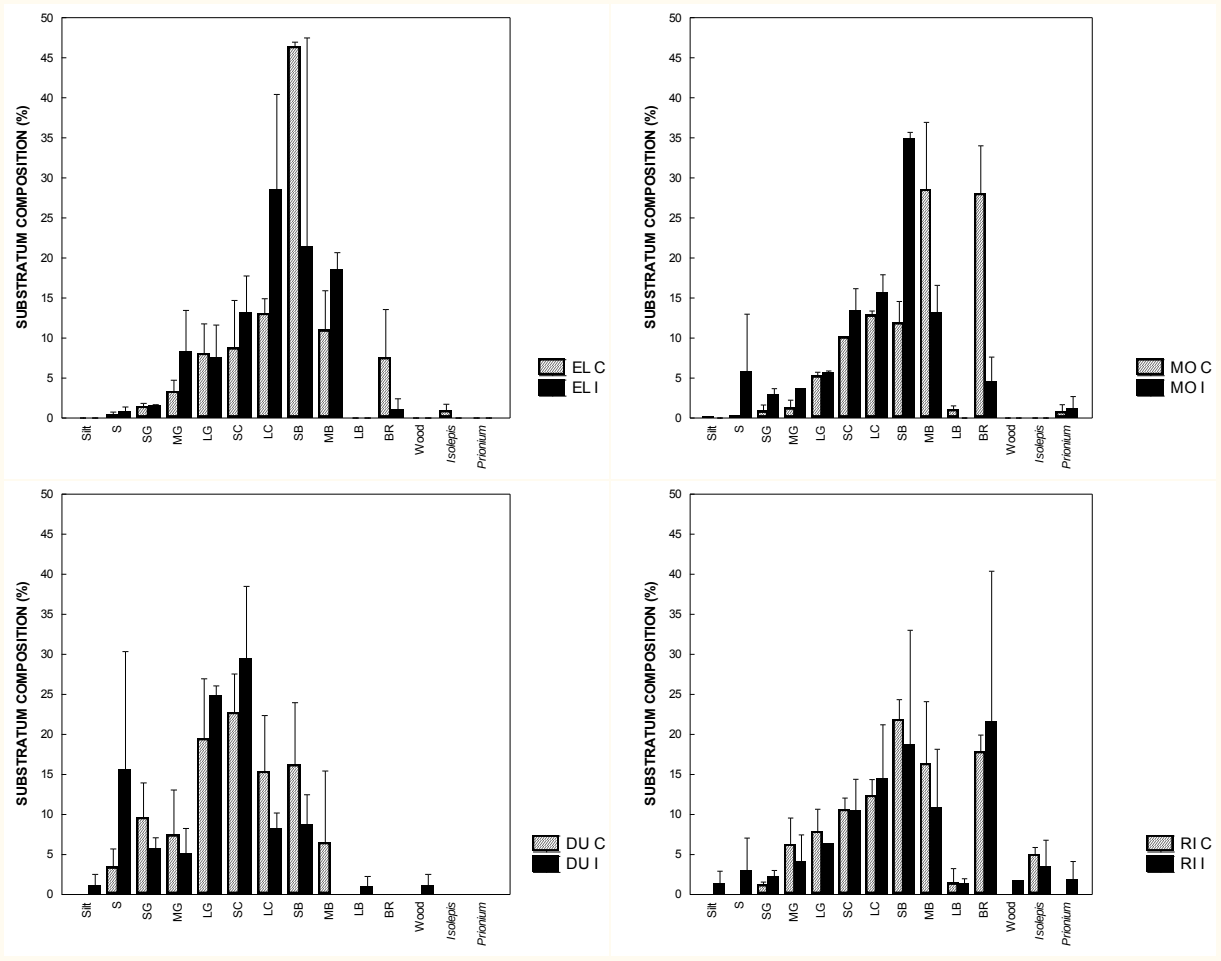


Figure 6.29 Substratum composition at the control (C) and impact (I) locations at sites. EL - Elands; MO - Molenaars; DU - Du Toits; RI - Riviersonderend. Standard deviations for means are indicated by error bars. Substratum grades: S - sand; SG/MG/LG - small/medium/large gravel; SC/LC - small/large cobble; SB/MB/LB - small/medium/large boulder; BR – bedrock. Wood - woody debris.

In terms of non-mineral substrata, the Riviersonderend showed the highest total percentage, at 6% of the total substratum, with less than one percent of the river bed comprising vegetation at the other sites (Figure 6.29). Woody debris (e.g. roots, branches of riparian fynbos) was observed at only the Riviersonderend and Du Toits sites, in small amounts (< 1%). *Prionium serratum* was found marginally and instream in similar proportions in the Molenaars and Riviersonderend reaches. *Isolepis digitata* was the dominant form of instream vegetation in the Riviersonderend River (4%), but only occurred in a small proportion at one other site, the Elands. Differences in the proportions of types of vegetation were recorded for the locations at each site, with the entire absence of one or more classes in some instances.

6.6.2 Biotope substratum conditions

The majority of biotopes, including those from which invertebrates were sampled, comprised predominantly small cobble to small boulders (Table 6.30). Runs and riffles were the only biotopes that consistently included larger bed elements, though pool bottoms included medium-sized boulders. Interestingly, trickle runs were dominated by small, largely exposed, boulders (55%), largely explaining the unique hydraulic characteristics observed for this biotope (Section 6.4). Small proportions of sand (max. 10%) were recorded for all biotopes, except areas transitional between riffles and runs. As indicated in Table 6.30, silt did not comprise a significant proportion of the river bed for any biotopes (probably as the month of assessment, December, experienced elevated flows). Silt (along with organic detritus) and leaf litter were rated as a separate component ('% other') in the field, however, as they were prevalent in backwaters, standing waters and other pools, and to a lesser degree, runs.

For the main biotopes, the percentages of fine and coarse, organic and inorganic particulate matter associated with individual components of the substratum were assessed, in combination, with anticipated differences in the quantity of detritus possibly affecting invertebrate composition and micro-distributions (Chapter 7). Only samples representing natural low flow conditions were analysed, with data pooled for all sites (and locations) and months. Findings are presented in Table 6.31.

For entire stones, there were no significant differences in the dry mass of epilithic material among hydraulic biotopes, with an average DM_{total} across all biotopes of 0.560 ± 1.238 g 0.1 m^{-2} (Table 6.31). In contrast, the dry mass of the organic fraction collected from stones in different biotopes differed significantly; runs differed most from the other biotopes in possessing the lowest mean value. The percentage represented by the organic fraction for each stone was similar irrespective of biotope type, at around 43%. Comparison of DM_{total} for upper substratum stones (W - whole) with the underlying substratum (U) showed that values were roughly an order of magnitude higher for the latter component, for all biotopes, especially pools. For $DM_{organic}$, the difference, again apparent for pools (but not for runs or riffles), was principally due to the accumulation of silt, leaf litter and other detritus in low-velocity and/or deep channel areas. The proportion accounted for by silt and other inorganic material was consistently a little higher for the underlying substratum than for the uppermost bed elements.

Table 6.30 **Substratum composition of different biotope types.** Avg - average; SD - standard deviation. Dominant size classes are shaded. Silt and other fines occurred in association with other substratum classes for most biotopes, especially standing waters (stand), pools and pool/run transitions, but were < 0.5% as an independent category.

BIOTOPE TYPE	STAND		POOL		POOL/RUN TRANS		TRICKLE		RUN		RIFF/RUN TRANS		RIFFLE	
CLASS	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD	Avg	SD
Sand	1.3	3.5	1.7	4.1	1.5	3.4	10.0	14.1	2.0	8.2			0.6	5.2
Small gravel	2.5	4.6	10.0	24.5	17.5	14.6	12.5	17.7	3.3	9.3	4.1	9.2	1.4	5.0
Medium gravel	12.5	35.4	1.7	4.1	18.0	17.4	12.5	17.7	6.0	12.6	5.7	10.3	6.6	14.4
Large gravel	19.4	17.4	14.2	24.6	21.0	26.0			14.5	18.8	16.4	21.8	12.0	19.2
Small cobble	23.8	21.8	26.7	37.6	20.0	16.8	10.0	14.1	20.6	26.6	18.2	21.9	24.1	26.4
Large cobble	21.9	29.0	21.7	16.9	17.0	25.3			19.8	25.5	23.6	40.1	20.9	26.0
Small boulder	18.8	37.2	12.5	20.9	5.0	10.8	55.0	35.4	20.8	29.3	30.9	45.9	22.4	32.2
Medium boulder			11.7	20.4					8.6	24.7			5.8	18.3
Large boulder									0.5	3.5	1.1	3.8	0.6	3.7
Bedrock									3.2	15.0			4.6	17.0
Isolepis									0.9	8.8			0.9	8.3

Stone tops showed significantly higher (and more variable) DM_{total} and $DM_{organic}$ averages for pools, than for runs or riffles (Table 6.31). In contrast, the quantities of total and organic material located on stone undersides (hydraulically more sheltered than tops) were significantly higher for riffles than for the other two biotopes, where average figures were similar. Examination of the substratum underneath the upper stone layer revealed significantly elevated amounts of detritus for depositional pool environments (mean total and organic fractions of 6.918 and 0.945 g 0.1 m^{-2}, respectively), as compared with riffles and, in particular, runs. The figures obtained also far exceeded those of the other substratum components. The percentage of the detritus comprising organic material was fairly stable, ranging from a $mean_{min}$ of 28% for riffles (U) to a $mean_{max}$ of 49% for pools (stone tops), across all substratum parts, with only riffles and pools showing significant differences, for stone undersides.

Table 6.31 Mean (± SD) total dry mass (DM_{total}, g 0.1 m^{-2}) of detritus, the dry mass of organic material present ($DM_{organic}$, g 0.1 m^{-2}), and the proportion represented by the organic fraction ($\%_{organic}$), collected from whole stones, stone tops, bottoms and the underlying substratum, in different biotopes. Significant results based on Kruskal-Wallis ANOVAs by ranks indicated by asterisks. *N* - no. of samples for each analysis and biotope. *Post hoc* multiple comparisons were used to identify which biotopes were significantly different (shaded). SIG - significant difference between only riffles and pools. DIFF - inconclusive *post hoc* test result.

SUBSTRATUM COMPONENT AND VARIABLE	H	*P*	RIFFLE	RUN	POOL
Whole stones					
N			52	32	30
DM_{total}	0.152	0.927	0.673 ± 1.517	0.468 ± 0.857	0.461 ± 1.048
$DM_{organic}$	6.509	*0.039	0.105 ± 0.113	DIFF 0.055 ± 0.058	0.156 ± 0.398
$\%_{organic}$	5.075	0.079	46.031 ± 15.4	37.078 ± 17.5	45.291 ± 17.2
Stone tops					
N			68	48	41
DM_{total}	27.409	***0.000	0.112 ± 0.223	0.098 ± 0.159	0.983 ± 2.903
$DM_{organic}$	38.650	***0.000	0.047 ± 0.112	0.022 ± 0.026	0.228 ± 0.634
$\%_{organic}$	4.438	0.109	49.0 ± 20.9	40.5 ± 21.8	49.1 ± 23.1
Stone bottoms					
N			63	51	44
DM_{total}	27.411	***0.000	1.090 ± 2.340	0.257 ± 0.472	0.208 ± 0.286
$DM_{organic}$	20.661	***0.000	0.120 ± 0.148	0.049 ± 0.047	0.076 ± 0.105
$\%_{organic}$	6.891	*0.032	SIG 33.2 ± 24.2	40.1 ± 21.5	SIG 44.4 ± 20.9
Substratum underlying stones					
N			51	45	29
DM_{total}	9.081	*0.011	4.673 ± 9.297	4.159 ± 8.941	6.918 ± 9.000
$DM_{organic}$	25.121	***0.000	0.165 ± 0.374	0.139 ± 0.171	0.945 ± 1.315
$\%_{organic}$	0.673	0.714	28.3 ± 29.7	33.3 ± 31.1	30.3 ± 29.1

6.7 SUMMARY AND DISCUSSION: PHYSICAL HABITAT DYNAMICS AT LOW FLOWS AND POTENTIAL FOR INFLUENCE ON INVERTEBRATE ASSEMBLAGES

Both natural and manipulated, extreme flow reductions led to distinct declines in the spatiotemporal availability of wetted habitat, coupled with changes in its hydraulic character, supporting conceptual low flow-habitat models (e.g. Lake 2000) and augmenting the quantitative evidence base for perennial rivers (Section 6.1). The magnitude and nature of this short-term habitat-discharge response differed depending on the spatial scale at which physical habitat was examined, with flow disturbance at finer patch scales clearly influenced by higher-level geomorphic filters. Thus, the vital importance of considering reach physical habitat within a spatially nested geomorphological hierarchy (Frissell *et al.* 1986; Minshall 1988; Rowntree and Wadeson 1999; King and Schael 2001; Section 1.4.7) was evident.

In conjunction with natural differences in low flow regime (Chapter 4), variations in channel geomorphology and associated habitat heterogeneity among and within river reaches (though minimised at the outset - Chapter 2), also measurably affected the strength and type of flow-habitat relationships observed. The combination of data from different reaches, or from cross-sections of differing morphology within them, thus typically yielded poorer results than independent consideration of river reaches or analyses of more homogenous aggregates of habitat patch types. Certain physical habitat variables from within the diverse range examined were more discharge responsive and thus potentially more appropriate surrogates for biotic response to flow disturbance than others. This result did not necessarily confer on such measures any greater power in explaining variation in invertebrate assemblage composition at low flows, or ecological relevance in terms of low-flow disturbance, but they were typically within the group of most influential factors (Chapter 8).

6.7.1 Responsiveness of channel-width descriptors of wetted habitat to low flows

Wetted width and perimeter, and low flows

Wetted width declined with decreasing discharge magnitude, as expected (Leopold and Maddock 1953; Tennant 1976; Bovee and Milhous 1978; Stalnaker *et al*. 1989; Davis and Barmuta 1989; Singh and Broeren 1989; Gordon *et al*. 1992; Crisp 1995; Jowett 2003), but more weakly tracked site flow patterns (Section 4.4) than did wetted perimeter, with which it is intimately related (Gippel and Stewardson 1998). Moreover, discharge-width trends were only distinct when individual river reaches, or transect types within them, were considered independently, in large part due to variation introduced by channel morphologies. Even locally within a reach, bed heterogeneity diminished the degree of flow-responsiveness detectable, as exemplified by the lack of a flow-related trend for riffle width, for the most severely flow depleted river section.

Variations in discharge-width relationships were similarly attributed to differences in channel form by Tennant (1976), for streams in the U.S.A., and by Jowett (1998) for a range of New Zealand river channels.

Both local channel geomorphological character and water volume also led to reach-scale differences in the degree of wetted habitat loss with severe drought in a small North American stream, Smiths Branch (Larimore *et al*. 1959). Numerous other studies have demonstrated that discharge reduction, natural or artificial, typically resulted in decreased wetted width (e.g. Kraft 1972; Gore 1977; Taylor 1983; Cowx *et al*. 1984; Wright and Berrie 1987; Bickerton *et al*. 1993; Englund and Malmqvist 1996; Stanley *et al.* 1997; Padmore 1997; Gippel and Stewardson 1998; Jowett 1998; Dewson *et al*. 2007a, b; McIntosh *et al.* 2002, 2008; James *et al*. 2009). Conversely, for example, Snaddon and Davies (1998) reported a threefold increase in wetted width with an unnaturally elevated (+4500%) dry season discharge in a South African river. These studies highlighted considerable variation in the degree of change in wetted width, again often explained by natural variations in channel morphometry.

Typically in the present study, non-linear decreases in wetted width with declining discharge were more strongly evident for run than riffle channel sections, and where marginal standing waters were included in regression analyses. As envisaged, with manipulated extreme flows, losses in wetted width became most pronounced at 22% and 15% for run and riffle transects, respectively, and at a time when widths were already naturally at their narrowest. Experimental discharge reduction of on average 89-98% (significantly lower than natural flows) for over one month, in riffle-dominated sections of Booths Creek, Kiriwhakapapa Stream and Reef Creek, New Zealand, resulted in similarly substantial losses in wetted width to those of the present study, of 24-30%, as compared with pre-diversion widths, in all of the narrow (< 4 m) streams (Dewson *et al*. 2007b). As to be expected, similar manipulated flow reductions in a longer-duration experiment in the same streams resulted in comparable wetted width declines of 22-38% (Dewson *et al*. 2007a; James *et al.* 2009). Wetted width similarly declined non-linearly with decreasing discharge in 11 U.K. streams, for riffle morphological units (and more so than for pool units), with greatest losses apparent at flow percentiles indicative of naturally very low flows (Padmore 1997). Englund and Malmqvist (1996), in an analysis of 24 rapid-dominated river sites in Sweden subjected to flow reduction, found a positive non-linear relationship between the percentages remaining of discharge and wetted width.

In the current assessment, wetted perimeter was more strongly positively dependent on discharge overall (R^2 = 0.67) than was wetted width, with a naturally accelerating downward trend with greater flow reduction (power function). With manipulated discharges below the lowest figures on record, marked losses in wetted perimeter and hence, potential invertebrate habitat, occurred in all reaches and were especially apparent for the most flow-impacted location (Riviersonderend site). For these small to moderately sized rivers, the greatest relative WP decline occurred below approximately 75% of the maximum recorded for the low flow season. Values below 50% indicated major losses in wetted habitat, as the cross-sectional shape and length of remaining wetted perimeter altered with substratum exposure (Newbury 1984). Stalnaker and Arnette (1976) similarly found for some U.S.A. streams that at 80% of maximum available wetted perimeter there were distinct breakpoints in Q-WP curves.

Both riffle and run transect biotopes were also far more responsive in wetted perimeter with discharge reduction (R^2 values between 0.49 and 0.99) than in width. Wetted perimeter lost as potential benthic habitat for run sections reached as much as 69% at flows well below absolute minima (Riviersonderend reach). Riffles tended to shrink less in wetted perimeter and in a more linear fashion than did runs (as also observed for wetted width), but still by up to 50% once discharges became unnaturally low (for two of the three experimentally diverted reaches). These results suggested that riffles, in particular, had already diminished considerably (at least in lateral extent) with natural levels of flow reduction mid-dry season, with remaining habitat approaching a naturally stressful threshold for the benthos (O'Keeffe *et al*. 2002).

Hollands (1998) reached a similar conclusion in a study of discharge-wetted perimeter relationships for nine anthropogenically least-disturbed southwestern Cape rivers (which included all four of the current study sites) that aimed to identify Q-WP curve breakpoints, for riffles and runs for each perennial reach, that might reflect low flows at which wetted bed shrinkage was most pronounced. Standardised discharges indicated by the identified breakpoints, termed Wetted Bed Flows (WBFs), ranged narrowly between 0.86 (40th flow percentile) and 1.12 (53rd percentile), on average approximating Q_{47} (approaching the accepted boundary of low and high flow regimes; Smakhtin 2001). Furthermore, average WBF expressed as a factor of the mean dry season runoff was in the order of 120%. Thus, for about half the year, river flows were below the WBFs, with significant wetted habitat loss already having occurred by the onset of the dry season, a natural phenomenon to which invertebrate assemblages were presumed adapted.

Distinct losses in wetted perimeter with decreasing discharge have been demonstrated in other studies, with the shape of the Q-WP relationship also a function of channel geometry and the way in which discharge increases with depth (Bovee and Milhous 1978; Nelson 1980; O'Shea 1995; Gippel and Stewardson 1998). In an application of a discharge-wetted perimeter approach to streams in Victoria, Australia, Gippel and Stewardson (1998) used wetted perimeter (and channel area with current velocity > 0.01 m s^{-1}) as direct measures of invertebrate habitat. Logarithmic (typical of rectangular channels) and linear relationships between mean wetted perimeter and discharge were derived for two headwater streams in the same region, Starvation and Armstrong creeks, respectively, where the latter site possessed the more variable channel morphology. Based on these trends, the predicted effects of an historical severe summer drought, which resulted in the absolute minimum (unregulated) discharges on record (Q_{min}), were liable to have been more pronounced in Armstrong Creek, where up to 29% of the bed would have been exposed, versus 16% in the narrower Starvation Creek; in comparison, Q_{95} would have provided at least 76% and 92% of maximum available wetted channel area at the same sites, respectively. Even under extreme flow conditions, therefore, a substantial amount of wetted habitat was predicted to remain for biota (e.g. 68% of maximum WP at zero discharge in Armstrong Creek) as non-flowing pools.

Changes in hydraulic character at channel-width scale with discharge reduction

Distinctive patterns in cross-channel hydraulics and associated relationships with discharge at low flows were more readily discernible for individual river reaches and transect types, reconfirming the important influences of the observed natural variability in physical habitat structure and low flow regime. The posited role of flow variability in enhancing habitat diversity (Jowett and Duncan 1990; Tharme and King 1998; Padmore 1997; Bunn and Arthington 2002; Postel and Richter 2003) was supported by greatest variability in hydraulic habitat being evident for the most flow variable reach, the Riviersonderend, leading to similarly highly heterogeneous riffle and run cross-sections. Conversely, under its naturally less variable and more predictable long-term flow regime (Chapter 4), the Du Toits site exhibited fairly uniform riffle and run profiles of comparatively low architectural complexity (Robson 1996; Robson and Barmuta 1998).

As anticipated based on various studies (e.g. Davis and Barmuta 1989; Wadeson 1996; Padmore 1997; Hollands 1998; Bouckaert and Davis 1998; Robson *et al*. 1999) riffle and run channel sections differed fundamentally in their hydraulic character, and distribution profiles (Armitage 1995) at natural flows, with attendant implications for invertebrate distribution patterns (Chapter 7). Riffles were consistently shallower (lower minima, maxima, and means), more turbulent, and exhibited higher and more variable (mean column and near-bottom) velocities than runs in the same reach, over natural low flow ranges. Hydraulic habitat conditions for invertebrates also differed in some fundamental respects among the different rivers. Shallowest and deepest riffles occurred in the Riviersonderend and Molenaars reaches, respectively. Runs were shallowest in the Du Toits River, while the deepest runs occurred at the Elands site. Lowest average velocities for riffles and runs also were encountered in the Elands reach, while the highest average and maximum velocities for both habitat types were recorded in the Riviersonderend River.

A reduction in discharge magnitude is understood to consistently reduce current velocity and water depth (Davis and Barmuta 1989; Gordon *et al*. 1992; Crisp 1995; Jowett 2003), with differences in channel width and substratum size influential in the degree to which wetted habitat is depth-limited (Gippel and Stewardson 1998) and velocity more affected by changes in discharge (e.g. Kraft 1972; Williams and Winget 1979, Armitage 1984; Leonard and Orth 1988). For example, Williams and Winget (1979) reported that velocity changed more than did wetted width or depth with flow manipulation in the Strawberry River, U.S.A. In a further example, across six U.S. Minnesota streams studied by Aadland (1993), average velocity was more variable with discharge than was water depth.

Multiple studies have demonstrated decreases in velocity and depth with declining flows over a range of river types and sizes (e.g. Minshall and Winger 1968; Kraft 1972; Gore 1977; Williams and Winget 1979; Extence 1981; Taylor 1983; Cowx *et al*. 1984; Wright and Berrie 1987; Bickerton *et al*. 1993; Malmqvist and Englund 1996; Wadeson 1996; Padmore 1997; McIntosh *et al.* 2002, 2008; Dewson *et al*. 2003; Dewson *et al*. 2007b; James *et al.* 2008), with the degree of change dependent primarily on local channel morphology. Similar to the current study, major experimental discharge reduction (of 89-98%) to below

natural flows, for over a month in three New Zealand streams, caused declines in water depth and velocity (cf. controls), and that were greater than the recorded decreases in wetted width (Dewson *et al*. 2007b). Additionally, as in this study, the degree of hydraulic change was not necessarily proportional to the magnitude of flow reduction, but reflected flow distribution under different channel morphometries. Dewson *et al*. (2007b) reported that mean depth decreased by 28-64%, a similar percentage decline on average (57%) to that of velocity, but only significantly in two of the streams. Velocity, in comparison, decreased significantly by 50-62% across all three impacted reaches, with a maximum reduction of 89% in Kiriwhakapapa Stream. Similar manipulated flow reductions in a longer-duration experiment at a different time, in the same streams, resulted in comparable habitat losses relative to natural conditions, but with velocity losses greater, at 52-89%, and depth decreases only significant for one stream (Dewson *et al*. 2007a; James *et al.* 2009). Dewson *et al*. (2007b) noted that even with such marked changes in physical habitat at very low flows, there remained patches of suitably elevated velocity, such that conditions might not have been extremely stressful to invertebrates (which showed variable responses to the severe habitat changes; Chapter 7).

Experimental discharge diversion also led to decreased water-column velocity to 44-69% of initial velocity, and depth to 25% of the initial value (but no appreciable reduction in wetted width, due to channel geometry), in a small stream, Spring Run Creek, U.S.A. (Minshall and Winger 1968). Significant declines in wetted channel width, mean surface velocity and mean depth (as well as Froude number) were reported with flow diversion of 92 to 98% in two Hawaiian perennial systems, Iao Stream (McIntosh *et al*. 2002) and Waihee River (McIntosh *et al*. 2008); fast-flowing riffle areas were altogether absent in the flow disturbed river sections. Longer-term changes in wetted width (and total wetted surface area), as well as in current velocity and depth, have also been reported, for instance occurring over two years that encompassed severely reduced dry-season flows in naturally perennial reaches of the River Lambourn, U.K. (limiting habitat diversity for invertebrates; Wright and Berrie 1987). For the New Zealand Mangaterere and Raparapawai streams and Tamaki River under ongoing water abstraction, however, decreases in instantaneous discharge from above to below abstraction points (of -22% to -81%) did not consistently result in decreases in wetted habitat in terms of mean cross-sectional depth, current velocity or stream width (though conversely, an increased discharge of +363% in a fourth river resulted in increases in these habitat measures), because of their flat U-shaped channels (Dewson *et al*. 2003).

In the current study, the positive relationships between velocity and depth, and discharge magnitude, differed in degree for the two variables and by transect biotope type. Dependencies of both mean average velocity and mean water depth on discharge were strongly positive for riffles, as also demonstrated by Padmore (1997) for several English streams. With natural declines in discharge midsummer, the typically moderate declines in riffle average and maximum depths and velocities still represented marked changes for cross-sections that had already experienced measurable, seasonal habitat loss. Artificially severe low flows exerted more profound effects than natural low flows on riffle hydraulics, in concert with the significant

recorded losses in wetted habitat, with declines in average riffle depths of between 20 and 50%, and in mean average velocities from 17 to as much as 71%. The impact was most pronounced, especially for depth, for the reach with the most open, shallow channel (Du Toits River). Poff and Ward (1991) reported decreased mean depth and current velocity in a riffle of the upper Colorado River with experimental discharge reduction, but without a marked loss of riffle wetted habitat in summer (although an estimated 10% of riffle surface area became partially exposed with discharge reduction in autumn).

For run transects, relationships between discharge magnitude and both mean average velocity and mean water depth were similarly strongly positive, and to a greater extent than for riffles. Extreme flow reductions resulted in major hydraulic changes, with decreases in average run depth and velocity of as much as 59% and 83%, respectively. The latter maximum decline in velocity (recorded for the Riviersonderend reach) was the most substantive of all flow disturbance effects on mean channel hydraulics, eliminating all high velocity areas, and with even the few remaining deeper sections approaching flow cessation (see also below; resultant effects on water quality and vegetation are discussed in Chapter 5).

Comparative studies of transect-based response of runs and riffles to low flows for direct comparison with this study's results were scarce. Kraft (1972) found that controlled three-month diversion of 90% of the normal discharge in Blacktail Creek, Montana, U.S.A., in comparison with 20% natural flow reduction for control sections, reduced wetted surface area and average depth more for run than pool transects. Conversely, the decline in mean-column velocity was greater for pools than runs, and average velocity decreased more than maximum velocity. Wetted surface area and average depth were least affected by severe flow reduction, due to a well-defined stream channel geometry, decreasing about 42% overall on average for pools and runs, while velocity decreases ranged between 71 and 85%. Different relationships with discharge were also shown for riffles and pools by Orth and Leonard (1990).

Observed changes in specifically the proportions of extremely low velocity to non-flowing waters (using the derived variable, $v \leq 0.01$ m s^{-1}) and extremely shallow waters ($d \leq 0.05$ m), across riffles and runs, under the different low flow regimes of the present study were of potential importance for flow-impacted invertebrate assemblages (Chapters 7 and 8), because of natural differences in hydraulic tolerances among taxa (Merritt and Cummins 1984; O'Keeffe and Dickens 2000; O'Keeffe *et al.* 2002; Picker *et al.* 2004). Even under natural flow patterns, invertebrate assemblages were subjected to sometimes marked, temporal variability in the proportions of shallow, non-flowing habitat. Flow manipulation to severely low levels resulted in dramatic linear or, more commonly, logarithmic increases in the proportions of extremely shallow waters, strongly correlated with the magnitude of discharge reduction. Similarly high maxima of 72% and 67% were recorded for riffles and runs, respectively, both in the Du Toits reach; as a result, the hydraulic distinction between these two transect biotope types became less apparent in this river at such flows.

Proportions of non-flowing water also showed distinct relationships with discharge, though weaker than those for depth. Areas showing flow cessation were particularly pronounced in the two most flow altered locations, reaching maxima of 41% and 70% for riffles and runs, respectively, at one of the sites. Gippel and Stewardson (1998) similarly showed strong logarithmic relationships between mean flowing water perimeter (defined as areas of velocity > 0.01 m s^{-1}) and discharge for both Armstrong and Salvation creeks in Australia, which led them to consider flowing perimeter more appropriate than standard wetted perimeter for defining suitable invertebrate habitat. Further, Rhodes (1994, cited in Gippel and Stewardson 1998) demonstrated that the most obvious effect, on regulated Australian headwater streams, of major discharge diversion by ten small weirs was a reduction downstream in the area of stream channel with a mean velocity above 0.4 m s^{-1} during abstraction periods (with adverse impacts on invertebrates preferring high-velocity habitats).

6.7.2 Classification and flow-related hydraulic characterization of biotopes

Although the above responses to extreme low flows in simple, channel-width measures of wetted habitat and hydraulics represented severe physical disturbances with the potential to alter invertebrate distribution patterns (Section 7.1), they revealed less about possible impacts to the benthos than biotope analysis, especially when the latter was patch-based rather than at transect scale.

Response to low flows at transect biotope scale

Total biotope length (TBL), calculated as the total channel-wide wetted patch length, excluding exposed areas, was a flow responsive measure of habitat availability that correlated strongly with discharge and steeply declined below about 70% of maximum. Similarly strongly positive relationships were found for riffle, and to a greater extent, run transects. The heightened responsiveness of run total wetted length to low flows again highlighted the likelihood that riffle sections, as erosional environments (Padmore 1997), were primed at natural low flows, having already lost considerable habitat outside of the dry season. Natural losses in TBL for riffles and runs at low flows were slight to moderate within all reaches, but once discharges were reduced to around or below absolute flow minima losses became significant, down to only 44% of habitat remaining and then of highly altered quality. Indeed, for the two most flow-impacted reaches, very few small riffle patches (only two, in the Riviersonderend R.) remained during the period of extreme low flows, and the few runs not converted to pools were extremely shallow and slow-flowing.

Even though habitat availability, as total biotope length, varied to a limited extent under the natural low flow regimes at sites, shifts in within-transect, patch (i.e. cell) biotope composition still occurred. These shifts became exaggerated with progressive discharge reduction, as TBL decreased and hydraulics altered, and were most pronounced when discharges changed from natural to extreme lows, or with the incidence of high flow events at summer's end. Riffle transects exhibited more complex and pronounced variability in patch composition (including degree of dominance by riffle flow types) and flow-related response than runs, commensurate with the former's greater heterogeneity. As also found with more detailed patch dynamics

analysis (see below), most typically sequential shifts in the proportional dominance of different biotope patches occurred with flow reduction. The shifts were from deeper and/or higher energy patches (e.g. riffles) towards lower energy, slower velocity and/or shallower biotopes (e.g. shallow runs, pools), with increasing substratum exposure and finally, partial streambed dewatering.

Changes in biotope proportions were particularly dramatic in highly flow-impacted locations, because they occurred within a smaller amount of remaining wetted habitat width and with a concomitant shift in hydraulics to markedly lower depths and velocities than occurred naturally. In extreme cases, with artificial discharge reduction far below historical minima, whole-scale transformation of the transect biotope type resulted, persisting throughout the disturbance period. Such transformation occurred from riffle to shallow run, with substantial bed exposure and the loss of those flow types characteristic of riffles, as well as from run to wholly pool-run environment. At the other end of the low flow spectrum, for the river exhibiting the most pronounced changeover to higher flows at the end of the dry season (i.e. Riviersonderend), elevated discharge triggered a natural change in transect type for one of the transects studied, from shallow run to deep, fast-flowing riffle.

In one of few equivalent studies available, Kraft (1972) found similar and pronounced shifts in the proportional representation of different depth-velocity categories (i.e. shallow-slow, deep-slow, shallow-fast, or deep-fast 'water-types', with 'fast' > 0.30 m s^{-1} and 'deep' > 0.5 m) for pool and run cross-sections. The transects were mapped over a range of low flows occurring with controlled diversion of 90% of normal discharge for an extended three-month period (cf. 20% natural flow reduction in control sections), in Blacktail Creek, Montana, U.S.A.; riffles were not examined. With only 10% of normal discharge remaining, there was an overall change from dominance by fast-velocity areas (over 60% of wetted surface area at natural flows) to slow-water areas, with such patches occupying over 85% of the stream area. Deep-fast areas, which comprised 20% of total surface area at normal flows, were eliminated across run transects and severely reduced for pool sections. Additionally, as in the current study, shallow-fast areas were altogether dramatically reduced or eliminated. While deep-slow proportions remained similar to those at natural flows, shallow-slow portions increased with the extreme flow reduction, from about 30% at normal flows to about 85% of total surface area.

When Rowntree and Wadeson (1996) examined biotope dominance at various discharges for different channel-width morphological units in the Buffalo River, South Africa, they found the same kinds of shifts in within-unit dominance due to flow change as those identified in the present study for multiple rivers. For all pool morphological units, for instance, pool patches dominated at the three lowest discharges (flow percentiles of 92, 73 and 50), but there was a significant increase in runs at the highest flow (Q_3). Interestingly, at low flows, riffle morphological units also comprised mainly pools, with riffles only becoming dominant at Q_{50} and supplanted by runs at the highest observed flow – both whole-scale transformations akin to those found in this study.

In perhaps the most directly comparable analysis, by Padmore (1997, 1998) across 11 river sites in England, with biotopes classified at meso-scale based on dominant flow type, the proportion of channel wetted width occupied by the dominant biotope also varied by site and discharge. In that study, discriminant analyses at transect scale highlighted the risk, however, of marginal or secondary biotopes of potentially high ecological value being under-represented (e.g. marginal deadwaters, which may act as flow refugia, according to Lancaster and Hildrew 1993a, b) or overlooked (e.g. low-velocity 'slower' patches not being identified amidst 'faster' ones). Moreover, transect-level classification was inadequate for biotopes that exhibited a range of hydraulic conditions, such as transitional biotopes (e.g. run-rapid), or that tended not to span the entire channel (e.g. glides, runs). Subsequent classification of individual sample 'cells' (analogous with the 'cell biotope' unit) by flow type markedly improved results (Padmore 1997, 1998). This was an especially important outcome from the perspective of the current study, where the upper river reaches examined have heterogeneous channels with quite high proportions of secondary biotopes. Wadeson (1996, p. 86) noted too that as the scale of the hydraulic biotope is much smaller than the channel morphological unit, there is a need for "a cell by cell classification of hydraulic biotopes rather than a general classification of transects."

Characterization of hydraulic biotopes at patch scale: key hydraulic descriptors

Wadeson and Rowntree (1998, p. 145) emphasised that the classification of hydraulic biotopes is premised on "an intuitive assumption that flow type is a true reflection of hydraulic conditions in the water column and that flow type and substrate class together define an instream environment that has ecological significance". At the scale of the individual patch, all biotope types encountered in the field were robust in hydraulic character, within the domain of natural variability, based on discriminant function analysis of aggregate data and groupings reflecting different low flow ranges. Their representing relatively discrete, potentially biologically meaningful habitat units importantly allowed a high level of confidence to be placed in the biotope types with which invertebrate assemblages were associated in Chapters 7 and 8. That the biotope could provide a statistically sound vehicle with which to explore spatial and temporal habitat variability was also concluded by Newson and Newson (2000), facilitating its adoption as a standard instream habitat unit in the U.K. despite a lack of ecological validation at that time.

Of the diverse range of hydraulic indices examined, no single index sufficed to fully discriminate among or classify different biotope types at a single discharge, or across discharges, as also found by Wadeson (1996), Padmore (1997), and Vadas and Orth (1998). Moreover there was no distinct gain in using only complex derived hydraulic variables (e.g. shear velocity) over core ones (e.g. depth) (Section 3.4.4), as also concluded by Jowett (1993), with the best classification results generally due to some combination. Several hydraulic indices exhibited significant positive or negative intercorrelations reflecting their known interdependencies (see also Jowett (1993) who found particularly strongly positive correlations among Fr, VD_{ratio} and velocity).

Froude number was fairly consistently the single best discriminator of biotope type, especially at extreme low flows and at naturally elevated low flows; perhaps an unsurprisingly result, given this turbulence index is expressed in features such as standing waves at the water surface (Jowett 1993; Newson and Newson 2000; Section 3.4.4). Typically, however, Fr achieved greatest discriminatory power in combination with other hydraulic variables from among which water depth (particularly at natural low flows) and near-bottom velocity (NBV, generally a more useful hydraulic index at low flows than mean-column velocity) were particularly influential, followed by substratum median particle size. Other useful descriptors were the mean column velocity to depth ratio (VD_{ratio}), Reynolds number (Re), relative roughness (R_{rel}), relative exposure (RE), and a turbulence index (TI). The potential for Fr as a biotope descriptor had been demonstrated early on by Allen (1951, cited in Wadeson and Rowntree 1998) in studies where like habitats exhibited similar Fr values, and explored subsequently by other researchers (e.g. Statzner 1981a; Orth and Maughan 1983; Wetmore *et al*. 1990; Jowett *et al*. 1991; Jowett 1993; Padmore 1997, 1998; Vadas and Orth 1998; Kemp *et al*. 2000; King and Schael 2001; see a review by Wadeson 1996). Kemp *et al*. (2000), for example, showed that 15 of 16 functional habitats differentiated at 32 U.K. river sites (Section 6.1) exhibited a distinct distributional relationship with Froude number, sometimes with identifiable optima, providing evidence for the control of such habitats by hydraulic factors.

Separation among the different biotope types visually delineated in the field (for an aggregate analysis of all biotope types, flow conditions and rivers) based on the nine most influential hydraulic indices examined, was driven along a first axis of increasing turbulence (Fr) and NBV (together effectively representing 'hydraulic energy', *sensu* Wadeson 1996), which most clearly differentiated between low energy pools and other biotope types, coupled with a second axis reflecting increasing water depth, and to a lesser extent, Reynolds number (Re). The two axes explained a high proportion (97%) of total variance. Velocity to depth ratio further contributed to the discreteness of individual biotopes. Overall success in objective biotope classification (based on other standards, e.g. Jowett 1993; Wadeson 1996) using all hydraulic variables was moderate (65%), and was just marginally enhanced when only riffle, run and pool biotopes were assessed, probably due to the elimination of variability introduced by other biotope types, with substratum d_{50} gaining in relative importance to Fr in biotope differentiation; although analysis using only derived variables improved the classification success for certain biotopes, it diminished it overall. Runs were best distinguished (85%), contrary to the finding of Vadas and Orth (1998) that runs tended to be more susceptible to misclassification than other mesohabitats. They found the least misclassified mesohabitat types to be shallow pools (typically misclassified as pool-run types) and fast riffles (mostly misclassified as riffle-run categories), then medium pools and, less consistently, slow riffles.

Wadeson (1996) and Wadeson and Rowntree (1998) also verified the consistency of a matrix of hydraulic biotopes (Rowntree 1996), in terms of five of a broader suite of hydraulic indices reflecting average and near-bed conditions that showed an obvious pattern of variability across biotope classes (viz. Fr, Re, shear velocity, roughness Reynolds number, VD_{ratio}). Hydraulic characterization using aggregated data from five

sites at four discharges within the perennial Buffalo River system, Eastern Cape, South Africa, showed that of eight biotopes studied, including pools, runs and riffles, all except rapids and cascades could be considered hydraulically distinct from one another and typified by particular ranges in the variables considered (Wadeson and Rowntree 1998). As in this study, Fr most effectively discriminated among the majority of biotope types (though riffles and cascades, and rapids and cascades, were not significantly different as type pairs). In related work, Wadeson (1994, 1996) found that Fr remained the most reliable discriminator among biotopes, with shear velocity and roughness Reynolds number also useful indicator variables; shear stress, energy slope, relative roughness and roughness height, however, showed no useful pattern of variability across biotopes.

Vadas and Orth (1998) considered Fr and VD_{ratio} the most effective hydraulic variables for differentiating among various, visually identified mesohabitat types in the Roanoke River, U.S.A. When coupled with a further four of 12 original variables selected for their discriminatory power and generality (viz. depth, NBV, 0.6V, velocity shelter) they were used as the basis of a flow-dependent mesohabitat classification system. The system for streams and small rivers, the robustness of which was tested using misclassification analyses and comparisons with data from other studies on habitat types used by different fish guilds, comprised deep, medium and shallow pools; deep and medium runs; and slow and fast riffles, where all types were defined using quantified ranges in these six hydraulic variables. For instance, fast riffles were specifically classed as having depths between 0.20 and 0.50 m, near-bottom and average velocities above 0.35 and 0.60 m s^{-1} respectively, as well as Fr numbers above 0.35, a VD_{ratio} above 1.5 and velocity shelter values exceeding 0.15.

Within Padmore's (1997, 1998) study of 11 English rivers, characterization of flow types (on which basis physical biotopes were assigned) was similarly achieved using different combinations of hydraulic variables (all complex, viz. shear velocity, relative roughness, relative exposure, shelter index, turbulence index) and with Fr consistently the best single discriminator across all sites and discharges in aggregate. Shear velocity and turbulence index (TI) were the second and third most useful indices for discriminating across flow types. Reynolds number and roughness Reynolds number were excluded up front, due to their perceived poor discriminating capabilities. Vadas and Orth (1998) considered Reynolds number (and shear stress) poor discriminators among mesohabitats, showing similar values across different types and with the former index exhibiting high spatial variation within and among streams. Wadeson (1996), in a pilot study on the Great Fish River, South Africa, had found Re generally ineffective in differentiating among biotope types, but further investigation of the index for the Buffalo River system indicated that it was quite useful in determining differences in flow turbulence between lower energy biotope classes; review of the literature by Wadeson (1996) supported its potential for the characterization of different flow environments.

Padmore's (1997, 1998) finer-level focus on flow types rather than on hydraulic biotopes *per se* facilitated successful flow type classification across a range of sites and discharges in most cases, and probably largely

explained the higher percentages of correctly classified patches, as compared with the moderate success in the present study and weaker classifications obtained by Jowett (1993) and Wadeson (1996). As in all studies, however, some cases were still misclassified (threshold for classification success of 75%). For example, patches of 'rippled flow in marginal biotopes' were frequently classified as 'smooth boundary turbulent'. Patch misclassifications might also be attributed to occasional difficulties in the field in precisely ascertaining the substratum and flow type for a specific point (Minshall 1988). This was especially the case for high energy patches with localised hydraulic variability in the present study, a point also raised by Wadeson (1996), where a patch of hydraulically rough flow might comprise a number of smaller scale microhabitats of differing hydraulic character (Davis and Growns 1991).

The present and other studies discussed above confirmed that, in addition to differences in their hydraulic ranges and variability in individual hydraulic attributes, various mesohabitats and their constituent flow types were best characterized by different hydraulic variables. In this study, riffle patches in particular consistently showed a significant degree of divergence from pools in hydraulic character, not unexpectedly given that they represent extremes of a hydraulic continuum. Jowett (1993, p. 243, Figure 1), Wadeson (1996), Wadeson and Rowntree (1998), and Vadas and Orth (1998) also found particularly limited overlap between these two biotope types in hydraulic attributes.

Riffles were best characterized by high values of the hydraulic descriptors Fr, VD_{ratio}, and relative exposure (RE), as well as comparatively low depths. The first two variables in particular (as well as e.g. shear velocity, Reynolds number and roughness Reynolds number) were demonstrated by Wadeson and Rowntree (1998) and Vadas and Orth (1998) to decrease progressively, in means and variability in a mesohabitat sequence from fast riffles (and other high-energy biotopes), to slower riffles, runs, and then lower-energy shallow to deep pools. Alongside its average hydraulic conditions, the high variability in hydraulic ranges exhibited by the riffle biotope was speculated by Wadeson and Rowntree (1998), and this author, to be an inherent attribute of potential ecological relevance.

Runs typically showed hydraulic characteristics intermediate between those of riffles and pools, as similarly demonstrated by Jowett (1993) and Vadas and Orth (1998), for features such as Fr numbers and velocities, with greater (mean and median) depths than those of other biotopes and low RE values. While runs tended to be more similar in physical attributes to riffles than pools, as also observed by Pridmore and Roper (1985), Jowett (1993) and Vadas and Orth (1998), clearly the biotope class reflected too broad a range of hydraulic conditions with the fairly typical misclassification of both pools and riffles as runs pointing most to a need to differentiate between fast and slow runs and the adjoining biotope classes. Padmore (1998) did differentiate shallow from deep runs, because despite having the same flow type they had different distributions of hydraulic variables and therefore, potentially different roles as habitat for biota. Such findings are important given the natural relative dominance of runs by area, as compared with other hydraulic biotopes, under all

low flow regimes in this study, as well as their central role in the provision of wetted habitat for invertebrates at extremely low flows (Chapters 7 and 8).

As anticipated, pools, despite encompassing a variety of subtypes in this study, consistently exhibited very low Fr figures and velocities, coupled with predominantly low depths and high figures for relative exposure (many pools were marginal slackwaters, as opposed to deep channel-spanning units; cf. Vadas and Orth 1998). Vadas and Orth (*op. cit*.) also showed this mesohabitat type to have low boundary Reynolds numbers and values for velocity shelter, when compared with riffles. Further, they refined the type through its division into shallow, medium and deep subcategories based on differences in depth, in addition to other hydraulic factors. Wadeson (1996) and Wadeson and Rowntree (1998) found that at the same discharge, and for all hydraulic indices assessed, pools (including backwaters) exhibited a greater hydraulic consistency (i.e. more homogeneous and with lower hydraulic variability) than any other biotope. They postulated that this low variability might contribute to the comparatively low species richness often encountered in this biotope type. Trickle runs, which like pools gained prominence at extremely low flows in the current study, were hydraulically complex, due to the domination by largely exposed small boulders (Section 6.4) generating rough flow (high relative exposure and relative roughness), but with similarly very low depths, Reynolds numbers and shear velocities to those of standing waters.

Though transitional biotopes showed intermediate values for a range of hydraulic variables, likely in part due to the influence exerted on the local hydraulics of a particular patch by adjacent cells with different flow types (Padmore 1997, 1998), classification validated both pool-run and riffle-run transitions as independent biotopes. Though these biotopes did not display significant differences in Froude number with changing discharge, variability in turbulence was lowest at extreme low flows when pool/run transitions became more similar to pools and riffle/run transitions could no longer be readily distinguished from runs. Petts *et al*. (1999) similarly recognised riffle/run and run/pool patch types, in addition to riffles and pools when mapping biotope distributions at four River Babingley sites, U.K., based on velocity, depth and substratum features; specific criteria for these patch types and their hydraulic features (e.g. 'fast' to 'mod./slow' and 'slow') were not given. Kershner *et al.* (1992) also observed transitional areas between distinct riffles/runs or pools/glides to be a common feature, noting that although such transitions might differ little in slope from distinct adjoining mesohabitats, they might represent quite different habitats for biota.

Although natural differences in river scale and hydrological type arguably preclude consensus on limiting hydraulic values for those variables best delineating different biotopes, and restrict the utility of such an approach anyway, the ranges obtained for pool, run and riffle biotopes in the present study matched well with those obtained by Jowett (1993), Wadeson (1996), Wadeson and Rowntree (1998), and Vadas and Orth (1998); corresponding summary statistics for the hydraulics of related flow types are presented in Padmore (1997) and Newson *et al.* (1998). Despite such concurrences among existing hydraulic biotope (and similar) classifications across multiple rivers, refinement of types is clearly warranted to minimise common

classification inaccuracies while maximising information content. Vadas and Orth (1998) suggested five to eight basic categories of hydraulics for mesohabitat classification, for example, possibly with hierarchical stratification into meso- and macro-level habitat units to facilitate effective use of any additional categories.

It was envisaged here (and confirmed by results in Chapters 7 and 8), as it has been by other researchers (among them, Kershner *et al.* 1992; Wadeson 1996; Padmore 1997; Wadeson and Rowntree 1998; Newson *et al.* 1998; King and Schael 2001), that hydraulic or physical biotopes are biologically distinct, with the identification of those hydraulic variables most characteristic of a particular biotope (akin to the 'biotope-centroid' approach advocated by Tharme and King 1998) likely providing insights into its associated invertebrate fauna, expressly because hydraulic conditions are known to influence biotic distribution patterns (Section 1.4.8). Indeed, Padmore (1998, p. 29) stated that "Hydraulic characterisation of biotopes allows biotic assemblages to be inferred, based on the existing literature on species' preference or tolerance ranges, or field samples". Moreover, "Hydraulic biotopes should be classified in terms of both median values and variability so as to incorporate Hynes' (1970) contention that the greater the variability in the flow hydraulics, the richer the hydraulic biotope is likely to be in terms of the stream benthos" (Wadeson 1996, p. 86). Additionally, though some of the hydraulic indices reflecting near-bed conditions (e.g. shear velocity) were not strong abiotic discriminators of hydraulic biotopes, it is important to note that they might still be of relevance for invertebrates (Chapter 8).

Biotope-specific changes in substratum conditions at low flows

Although major shifts in substratum composition have been recorded during flood disturbance events (e.g. Lake *et al.* 1989; Cobb *et al.* 1992; Matthaei *et al*. 1997; Biggs *et al*. 1997; Silver *et al*. 2004) as expected, the river bed was stable at low flows, with no major changes in substratum composition or orientation. While appreciable increases in river-bed silt have been reported at very low flows (e.g. Kraft (1972), with 90% discharge reduction in Blacktail Creek, U.S.A.; Wright and Berrie 1987), silt accumulation was localised in this study. Substratum composition clearly was an influential element of benthic habitat (Newbury 1984). The distributions, sizes and durations of different patches (e.g. riffle and pool biotopes) and discharge-related shifts in hydraulics (e.g. depth and velocity distributions) at particular sites, were delimited by substratum attributes, as was the substratum type itself (Pringle *et al*. 1988).

Furthermore, substratum condition clearly affected nutrient retention and the accumulation of particulate matter (Pringle *et al*. 1988), with significant, natural biotope-specific differences in the proportions of silt and organic detritus. These materials were more commonly encountered in pools (followed by riffles, and then runs), depositional areas where they tend to accumulate at low velocities (Davis and Barmuta 1989; Lancaster and Hildrew 1993a; Wohl *et al.* 1995; Vadas and Orth 1998; Jowett 2003), altering microhabitat structure and reducing available habitat (Armitage 1984). Importantly in this regard, pool areas increased in relative importance as refuge habitat at drastically reduced water levels. The tops of stones in pools, but also interestingly riffle stone undersides, showed the highest amounts of total and organic detritus of all biotope

microhabitats examined, while runs typically showed the lowest detritus levels. Although in a mesohabitat analysis by Vadas and Orth (1998), runs trapped higher percentages of fines than riffles, the authors recognised the potential for high spatiotemporal variation in this factor. Leaf and wood fractions of coarse particulate organic matter were consistently more abundant in 'slow' than in 'variable' or 'fast' habitat patches, irrespective of discharge, in Lancaster and Hildrew's (1993a) study. Wohl *et al.* (1995) also reported differences among depositional cobble-riffle and bedrock habitat types in proportions of organic matter, current velocity and substratum character, in Wine Spring Basin, North Carolina, U.S.A.

From the perspective of the benthos, such inter-biotope and microdistributional differences in substratum character, as well as in short-term accumulations of fines and organic detritus at extreme low flows (Chapter 5 and Section 6.6) were indisputably important, for example in dictating the availability of food resources for detritivores in refuges in periods of low flow stress (Chapter 7). Lancaster and Hildrew (1993a) also highlighted the importance of considering the possibility that invertebrates might be responding indirectly to hydraulic conditions in a habitat patch through some other factor directly related to flow, such as leaf litter.

Influence of discharge variation on biotope character and dynamics

Although hydraulic biotopes are related to morphological features (Jewitt *et al.* 2001; King and Schael 2001), they are flow (hydraulic) rather than sedimentological units and hence, the assemblage of biotope types has been shown to vary with discharge across different river ecotypes. As a result, Wadeson and Rowntree (1998, p. 156) felt that "hydraulic biotope classification has potential as a tool for assessing discharge related changes in available habitat", though acknowledging that further validation was needed. Frissell *et al.* (1986) and Resh *et al*. (1988) postulated that variable levels of disturbance from different flow events might be expected across biotope types, due to factors such as differences in hydraulic characteristics and bed topography. The present study supported such views, with low flows exerting a range of degrees of disturbance across the biotopes examined.

Discharge variation and biotope character

In the present study, pool, run and riffle biotopes remained distinct entities across the spectrum of low flows examined (viz. discharge groups representing: (1) the higher end of the low flow range; (2) the natural range of midsummer discharges; (3) the discharge range representing manipulated flows below historical minima), although there was discharge-dependency in terms of their dominant hydraulic characteristics. Under conditions of naturally elevated low flows, and typical lower dry-season discharges, discrimination among major biotopes was most powerful using combinations of multiple core and derived hydraulic variables, with only two discriminant functions required to explain effectively all variance. Froude number, though the most influential variable under highest low flows (along with NBV, depth and RE), became considerably less so relative to water depth at natural very low flows (Davis and Barmuta 1989), when NBV, VD_{ratio}, Reynolds number and $SUBd_{50}$ were also key factors. Davis and Barmuta (1989, p. 280) observed that "Chaotic flows

may characterize certain habitats during dry periods" only to be replaced with other flow types as discharge and hence, water depth, increased.

Biotopes became even more discrete in terms of their fundamental hydraulic character within the range of discharges manipulated below historical minima than under natural low flow regimes (though significantly with a concomitant decrease in the strength of invertebrate-biotope and hydraulics associations - Chapter 8). The model for biotope response to extreme low flows exhibited the strongest discriminatory power of all biotope classification models developed, with only four derived hydraulic variables, principally Fr and R_{rel}, with lesser contributions by Re and VD_{ratio}; other important contributors to biotope differentiation in a similar analysis using both core and derived indices included 0.6V, $SUBd_{50}$ and TI. Classification was correspondingly most successful at such vastly reduced flows (86% overall, and reaching 98% for pools, which were poorly classified in the aggregate analysis), though some riffle patches were miss-assigned to runs and there was a marginally increased risk of misclassifying runs (recognized as containing a spatial mix of flow environments; Davis and Barmuta 1989) as pools.

Whether delineated primarily on the basis of hydraulics (biotopes) or invertebrate assemblages (functional habitats), other studies showed similar increases in patch distinctness with discharge reduction, suggesting that it may be most precise to model patches both at the lowest discharge possible, and again at highest flows. Armitage *et al*. (1995, p. 368) reported that distinct discontinuities among functional mesohabitats became apparent late summer as discharge declined to natural baseflows, also emphasising that mesohabitat borders were "best defined in low flow periods" (cf. Pardo and Armitage 1997, who reported that patch boundaries though variable, were more distinct at higher flows). Similarly, Wright and Berrie (1987), in a study of five dominant biotopes in the English River Lambourn, demonstrated least overlap among them during the dry season.

In contrast, Pardo and Armitage (1997) and Wood *et al*. (1999) observed a breakdown in pattern at extreme low flows, so that boundaries or physical discontinuities between habitats were reduced to gradients potentially acting as areas of habitat transition, and environmental homogeneity was created. For example, prior separation between 'fast' and 'slow' gravel samples was no longer evident, with 'gravel slow' shown to have affinities with both adjacent 'gravel fast' and 'sand' mesohabitats, in the former study. Wood *et al*. (1999) postulated that the response was associated with a reduction in channel width and water depth (and increase in fines), and the resultant decrease in total habitat availability. A decrease in variability in flow turbulence for all biotopes as flow diminished similarly implied increased spatial uniformity in a biotope study of the Great Fish River, South Africa (Wadeson 1996).

The increased delineation of major biotopes at artificially extreme low flows within a reach, as compared to typical low flows, here suggested that hydraulic barriers to invertebrate inter-patch movement might be potentially greatest in the former situation. Moreover, increased patch differentiation was not simply a

function of biotopes experiencing lower limits or variability in hydraulic ranges. Rather, it was due to multiple shifts in hydraulic character to which invertebrate assemblages would need to respond while already under low-flow stress. Such flow reduction effects were most pronounced for runs, with nine hydraulic indices exhibiting significant departures from corresponding values under natural low flows. In particular, run patches exhibited marked declines in depth and particle size (pointing to short-term, localised accumulation of fines, due to reduced velocities and increased plant decomposition; see above and Chapter 5), and increases in the ratio of velocity to depth, protrusion of bed elements with shallower water (a decrease in RE), and prevalence of smooth flow (decreased Re and R_{rel}). Riffles also showed highly significant decreases in water depth and increases in VD_{ratio} with the shift from natural to extreme discharges, as well as decreases in RE and Re. Additionally, Froude values were significantly higher for riffles at extremely low discharges than in other periods of low flow, and increases in R_{rel} and shear velocity were evident. In contrast, pools retained their basic character with flow diversion, though significant decreases in depth corresponded with similarly significant increases in relative exposure and flow roughness (and decreased pool connectivity, as discussed below). Further, Froude values were at their lowest values or zero, and with lowest variability, at extremely low discharges. Although pools appeared to provide fairly stable hydraulic conditions at all but the lowest discharges, it is noteworthy that they (and by implication their resident biota) have been found to be subject to greater disturbance than parts of riffles at high flows, due to elevated scouring velocities (Jowett 2003). Moreover, in a study of Timber Creek and Kyeburn Stream, New Zealand, pools were reported not only to have a higher disturbance frequency, but also a lower availability of refugia for biota than riffles (Scarsbrook and Townsend 1993).

Similar to the results for biotopes in this study, Padmore (1997) showed that flow types in 11 British rivers were characterized by different sets of hydraulic indices for three different discharge groups reflecting a range in flow percentiles from Q_{15} to Q_{100} (viz. (1) 'low', for summer drought flows; (2) 'mid', for moderate baseflows (Q_{35}-Q_{82}); (3) 'high', for winter high flows). Froude number (as in the present study) and shelter index were key variables for discriminating among flow types at naturally very low flows (at transect level) (RE and then Fr were the main discriminatory variables at moderate flows, while RE, TI and Fr were key indices for winter high flows). Classification success was greatly improved at cell level (equivalent to the biotope patches of this thesis), to approx. 95% of observations on average across flow types. Padmore (*op. cit.*) reported too that for pools (and other low energy biotopes) the distribution of Froude numbers was similar across all sites irrespective of discharge, with low variability. Higher variation and some degree of overlap in Fr values were noted for flow types typical of higher energy biotopes, though mean values remained similar at different discharges and sites.

In contrast with the above studies, Wadeson (1996) and Wadeson and Rowntree (1998) found the hydraulics of eight biotope types in the South African Buffalo River (all sites lumped) to be rather more consistent across discharges, based on different flows reflecting exceedence percentiles (%) of 3, 50, 73 and 92, though variability was apparent. Among-biotope differentiation at low (Q_{92}), intermediate (Q_{50} and Q_{73} combined)

and high (Q_3) discharges was most successful using four of the nine hydraulic variables examined, with inclusion of shear velocity and Reynolds number only marginally enhancing the classification success achieved with Fr and VD_{ratio}. Although average classification success was below that of this study and Padmore (1997), at 59%, as in this study it was also best at low flows. Though riffles (and other high-energy biotopes) showed high levels of hydraulic variability with discharge (as well inherently) there were no consistent flow-related trends, with differences in Fr and other hydraulic indices insignificant across discharges; a higher number of hydraulic variables was needed to more successfully delineate riffles than the other biotopes. At very low flows, runs were consistently more successfully classified than either pools or riffles. They were less sensitive than pools to small changes in discharge, with a high degree of hydraulic similarity across flows of different magnitudes, except for the highest discharge examined when they hydraulically closely resembled riffles (also pointing to a need to further differentiate in existing biotope categorizations between slow and fast runs, as well as to refine hydraulically the transition between run and riffle). Pools were poorly classified irrespective of the combination of hydraulic variables considered, and differed significantly in hydraulic characteristics (e.g. Fr, shear velocity, roughness Reynolds number) across discharge ranges.

Discharge variation and biotope dynamics

A number of common sequential changes in individual patch type occurred with discharge reduction across all reaches; progressions in patch type were identical to those of individual transect-biotope cells. Extreme discharge reduction resulted in clear shifts from higher- to lower-energy patch types, often with quite different hydraulics from the starting patch, as for example occurred with transformation of some riffle patches through riffle-run transitions and shallow runs, to trickle runs. Progressive dewatering also led to habitat isolation, with areas of partially or wholly exposed substratum as a common endpoint. Riffles transformed to run patches, in some instances with either increasing or decreasing discharge, while runs transformed into either riffles or pools, among other types. Pool patches were not recorded altering to riffles, nor the converse, highlighting the strong divergence between these hydraulic biotopes. Pools also showed the least diverse responses to decreasing discharge, though differing degrees of isolation were a typical feature of this patch type.

The biotope sequence and discharge at which transformation to another type occurred differed according to the starting (original) hydraulic character of each patch and the complexity of local bed topography (Figure 6.26), with direct bearing on the extent to which response to discharge alteration was detectable. Individual patch location and size also were central to the response observed. For example, a large mid-channel pool might remain a pool, although patch size, boundaries, and the hydraulics of smaller cells embedded within the larger patch might change, for example, as shown for riffles in the Great Fish River, South Africa, by Wadeson (1996). In contrast, a shallow marginal patch might transform into an isolated pool, and eventually standing water. As yet, few biotope dynamics studies have factored-in such considerations.

The sequences were consistent with and expanded upon flow-related changes in the hydraulic behaviour of patches identified by other researchers (e.g. Ulfstrand 1967; Kraft 1972; Kershner *et al.* 1992; Aadland 1993; Lancaster and Hildrew 1993b; Vadas and Orth 1998; King and Schael 2001), as well as predicted in the simple flow alteration-biotope transformation model of Rowntree and Wadeson (1998). Padmore (1997, p. 123, Figure 5.8) and Newson *et al.* (1998), for instance, reported similar generalised effects of drought and normal flows, based on studies of physical biotope sequences and temporal variability in the hydraulic character of individual biotopes at 11 U.K. sites across discharges ranging from Q_{15} to Q_{100} (three discharge groups: 'low', for summer drought flows; 'mid', for baseflow; 'high', for winter high flow). As in this study, they were able to identify relative thresholds of response of erosional and depositional biotopes or "transition probabilities between patches" (*sensu* Fisher *et al*. 1982, p. 99) with discharge reduction, although precise flow percentiles could not be determined.

When Lancaster and Hildrew (1993b) monitored the hydraulic behaviour of a subset of 150 of 600 small stream patches, classified into one of three types based on patterns of hydraulic stress (using FST-hemispheres; Statzner and Müller 1989; Statzner *et al*. 1991) and velocity, over a range of discharges in Broadstone Stream, England, they found a number of flow-related trends. The 50 'slow' patches consistently exhibited certain hydraulic features (i.e. low near-bed velocity and shear stress) irrespective of discharge. In contrast, although hydraulic stress was consistently high in the 'fast' patches, it was also significantly positively correlated with discharge. The remaining 'variable' patches showed a closer, significantly positively relationship with flow than the others, transforming from patches of low or undetectable shear stress and velocity at low discharges to patches with hydraulic characteristics similar to those of 'fast' patches at higher flows. These discharge-related responses in patch character influenced both their potential as flow refugia (Lancaster and Hildrew 1993a, b) and invertebrate distribution patterns (Chapter 7).

Differences in hydraulic biotope integrity and character across sites

Individual biotope types retained their integrity across all river reaches and with sufficient rigour, though riffles tended to be most poorly classified. Differences in classification success also disclosed weaker differentiation among biotope types in the uppermost river reach (viz. the Riviersonderend, and especially for pools) than for the other reaches, and strongest biotope delineation in the Elands River. Although Froude number remained an influential variable when individual sites were compared, depth, near-bed velocity and TI, as well Re and mean column velocity at extremely low flows, came more strongly to the fore as key indices. Those hydraulic variables most responsible for delineation among riffle, run and pool patches varied somewhat across the sites, probably reflecting the kinds of natural differences in channel form, morphological units and physical habitat heterogeneity discussed above. The implications of such limited site-to-site variation for biotope-invertebrate associations, as well as for habitat change and invertebrate response, are explored in subsequent chapters. With the shift from natural to abnormally low discharges, biotopes at individual sites still retained their integrity and to a heightened degree when compared with

pooled data. The result was most apparent for the Molenaars reach, which had the most moderate low-flow disturbance history (Chapter 4).

Padmore (1997) also reported few among-site differences in the hydraulic distributions for a particular flow type, which suggested a coherence to flow types as well that persisted regardless of location or channel morphology. Similarly, across multiple sites within the Buffalo River system, South Africa, for all hydraulic biotope types (using those hydraulic variables found to be the best biotope discriminators, i.e. Fr, shear velocity, roughness Reynolds number), inter-site differences were insignificant (Wadeson and Rowntree 1998). Although pool and riffle biotope classes showed some variability across sites for certain indices, the overlap was sufficient to consider the complete hydraulic biotope classification consistent over a range of channel scales, at least within that same river system.

6.7.3 Reach-scale biotope dynamics and diversity under different low flow regimes

The contraction and expansion of different biotope patches at reach scale, with changes in wetted surface area under different low flow regimes, generated new insights into relevant habitat-discharge relationships for invertebrates, especially given the recognised potential of the riverscape patch mosaic in influencing invertebrate distribution patterns (Section 1.4.6). As Stanley *et al.* (1997) commented, in developing a conceptual model of hierarchical patch structure that incorporated probabilities of differential patch loss associated with flow reduction, knowledge of those patch types most susceptible to shrinkage or desiccation with flow reduction and their properties assists with predicting the ecological implications of a decline or loss of that patch type.

Reach patch dynamics

The overall quantity of wetted habitat naturally available to invertebrate assemblages at low flows was commensurate with differences in river size and average discharge (being lowest and highest in the Du Toits and Molenaars reaches, respectively). Total wetted surface area was responsive to discharge fluctuation, with habitat shrinkage most pronounced with flow reduction to extremely low levels, though only distinctly for two of the three flow-impacted reaches. The Riviersonderend reach showed least evidence of a progressive reduction in wetted surface area with decreasing discharge, possibly due to factors including marked habitat loss prior to the peak dry season, its bed topography and naturally high proportion of pools, as well as channel form. The last factor, for example, limited the influence of stream bed dewatering with discharge reduction from normal to summer drought levels in Convict and Hunt creeks, U.S.A., to only approx. 3% of the bed exposed in each case, because of the entrenched nature of the channels (Hooper and Ottey 1988).

Though runs predominated in the study reaches irrespective of site or discharge magnitude (except in the case of the Riviersonderend R., where pools alternated with runs in dominance), differences in overall biotope composition were apparent across the rivers. This trend was also reported in Padmore (1997) and

Vadas and Orth (1998), as well as in Kershner *et al.* (1992) for the proportions and sequences of various fast-water to slow-water mesohabitats types among different U.S.A. stream reaches. In addition, Wadeson and Rowntree (1998) reported the same finding in their comparison of five reaches of the Buffalo River system. In contrast, Wood *et al*. (1999) found similar mesohabitat patterns in the English groundwater-dominated Mill Stream, Little Stour River and River Gadder, for three mesohabitats identified based primarily on substratum type, though all systems were anthropogenically modified and therefore, possibly simplified in physical habitat structure (King and Schael 2001).

As discharge, and hence wetted area, increases, new biotope (or other mesohabitat) classes are created and biotope proportions shift, and likewise with flow reduction, though some biotope classes are lost, proportional representation alters and additional types may emerge (Armitage *et al*. 1995; Wadeson 1996; Padmore 1997; Pardo and Armitage 1997). Somewhat counter to the prevailing view, therefore, that habitat conditions are very stable over the low flow period, biotopes were dynamic in the proportions they represented within each reach (supporting transect-level results), matching observed natural variability in low flow patterns. Artificially reduced flows considerably altered such dynamics, reinforcing natural trajectories of change in the proportions of patches of different types with decreasing discharge, with trends more strongly apparent when examined at individual sites rather than collectively across river reaches.

Pools and standing waters were present in small proportions and variable in presence or absence in any month or part of the reach represented by a site, rendering them less practical indicators of habitat-flow response than riffles, on a single-biotope basis. As a group, however, all low-energy pool-like environments (viz. standing waters, isolated and in-channel pools, pool/run transitions) usefully showed consistent and marked increases in availability in response to decreasing discharge. Moreover, pools became increasingly isolated within and along the channels as discharges decreased (notably, below Q_{inst}: Q_{50} = 0.2, for pooled data), with many implications of such losses of pool connectivity and potential flow refuges for invertebrates (e.g. Larimore *et al*. 1959; Pollard *et al*. 1996; Stanley *et al.* 1997; Lake 2000; Covich *et al*. 2003; see also Section 7.1). The degree of pool isolation was a particularly useful indicator of flow disturbance intensity, with the number and areal extent of entirely isolated pools (i.e. without contact with flowing water and sometimes stagnant) highest at extreme low flows (e.g. 0.4% to 4%, and none to 11%, from natural to abnormally low flows).

Higher energy patches showed the converse trend to that of pools, with riffle area particularly responsive to flow change. Riffles, typically viewed in other studies as critical habitat areas during low flow events because of their tendency to dry out ahead of other patch types (Hynes 1970; Ward 1976), declined most dramatically of all biotopes, from about 10% of reach wetted area naturally in the peak dry season to only 4% (Riviersonderend) or as low as 1% (Du Toits) with extreme discharge reduction. Its responsiveness made the riffle the most ecologically useful individual biotope type to track with flow change. As for low-energy biotopes, the combined response of riffles and other high-energy biotopes, of a decrease in reach

proportions with decreasing discharge, was a useful indicator of low flow-habitat response. Runs, though dominant, were more variable in response to discharge and with proportional representation increasing or decreasing from natural levels with flow reduction, as well as having the added uncertainties associated with the breadth of hydraulic conditions they reflected.

Buffagni (2001), in mapping discharge-habitat relationships for four hydraulically different functional habitats in the Pioverna River, Italy, at eight discharges from 0.01-1.20 $m^3 s^{-1}$, similarly found decreases in the amount of riffle area per unit reach length with decreasing discharge and maximal pool area at relatively low discharges. Aadland (1993) tracked the availability of six hydraulic habitat types, each characterized by specific depths and velocities (and each associated with a particular fish guild), over different discharges, for six Minnesota streams, U.S.A. Shallow pool habitat was dominant in area at low flows (decreasing at higher flows), while medium and deep pools were less responsive, changing little in area with changing discharge. Slow riffle area declined with discharge reduction, particularly from moderate to low discharges, and fast riffles became rare or absent at very low flows, as they did in the present study.

With seasonal flow reduction, Palmer *et al.* (1991) observed comparable shifts from erosional to depositional biotopes (e.g. riffle patches diminished in size or dried out leaving only remnant pools, and larger slow- to non-flowing depositional areas increased in representation) in the South African Buffalo River, associated with changes in flow hydraulics. Barmuta (1989), in a study of habitat-invertebrate associations in the Acheron River, Australia, reported a similar seasonally-driven change, with a decrease in the number as well as hydraulic transformation of depositional habitats (e.g. pools became rapidly flowing runs). There was a concomitant increase in the proportions of riffles and other erosional habitats with the shift to higher (winter) flows. Partial riverbed exposure at summer low flows, in contrast, resulted in a greater variety of habitats of differing areal extents. Changes in the proportions and diversity of five major biotopes in the River Lambourn, U.K., were noted over a more extended two year period that encompassed severe dry-season flows due to drought (Wright and Berrie 1987).

Stanley *et al.* (1997) in a multi-scale investigation of spatiotemporal patch dynamics associated with flow reduction in the naturally intermittent Sycamore Creek system, Arizona, U.S.A., also found different patterns of water loss and differential susceptibilities to drying of runs, riffles and pools at the reach scale. Overall reach shrinkage at low flows was a result of the contraction of individual habitat patches with high susceptibilities to drying. Over a 12 km creek section, regression analysis of water surface area in all riffles, runs, and pools, versus total wetted surface area showed that, similar to the current study, the greatest contraction in wetted habitat was attributable to decreases in riffle area. Previously submerged substratum elements became exposed and water was progressively trapped in depressions throughout the fragmenting riffle, as isolated pools. Water loss from pools was more gradual, with total pool surface area remaining fairly constant as this patch type proved more buffered from drying than either riffles or runs; runs were intermediate in desiccation susceptibility.

Protracted low flows in the perennial headwater stream, Quebrada Prieta, Puerto Rico, led to contraction and isolation of pools, with significant reductions in their mean and maximum depths and volumes, as well as complete drying of riffles (with associated loss of access to biotopes and microhabitats by invertebrates; Covich *et al*. 2003). With progressive discharge reduction during a severe drought in the Sabie-Sand River system, South Africa, Pollard *et al.* (1996) also monitored changes in the hydraulic characteristics of a number of different pool types, such as transient pools (lasting only for the first month), and persistent pools, either formed when the reach stopped flowing or isolated before flow ceased in the main channel. Increases in pool isolation were concomitant with marked declines in water depths and volumes (which could be related to changes in the persistence of invertebrate assemblages – Chapter 7). Riffle areas also showed clear decreases in depths and velocities, pre-desiccation and exposure. Notably, such flow-linked habitat losses were considered a more serious constraint for invertebrates than the simultaneous deterioration in water quality (Section 5.1).

Biotope patch number and diversity

While acknowledging the expediency of maintaining biotope diversity in the absence of a greater understanding of biotope-biota relationships, Padmore (1998, p. 34) concluded that "Until the ecological relevance has been established, and 'functional' habitats have been selected from the range of 'potential habitats' (Harper et al., 1992), the objective of river managers may be an 'act of faith' in maximising biotope patchiness and diversity." Though neither biotope patchiness nor diversity proved particularly useful individual measures of habitat change across the discharge range examined in this study, there was merit to examining both the range of types and number of patches in each river. At reach scale, patch heterogeneity based simply on the number of different patches, although in part a function of river size (and thus, greatest for the Molenaars River and lowest for the Du Toits site) was limited and, as also demonstrated by Padmore (1997), was clearly related to the degree of bed topographic variation.

Overall patch number showed no definitive response to discharge, but biotope-specific trends were apparent. Pool patches were most abundant at low flows and increased non-linearly in number as discharge decreased. Riffles and runs weakly showed the converse trend with flow, and with run patches less numerous, but far larger, than riffle patches. Average patch size (acknowledging that patch size frequency distributions can be highly skewed; With *et al*. 1997; Palmer *et al*. 2000) showed clear responses to discharge reduction that were dependent on the biotope type implicated. While losses in the extent of individual riffle patches occurred with flow reduction, pool patch sizes increased; runs did not show a consistent flow-related response.

Biotope diversity remained relatively high in terms of the number of different patch types over time and across sites, decreasing only slightly with diminishing discharge. Rowntree and Wadeson (1996) also studied hydraulic biotope diversity at different discharges, for a range of morphological units in the Buffalo River, South Africa, adopting a biotope diversity index derived from biotope diversity curves of the ranked

frequencies of biotopes for each morphological unit-discharge combination (which were compared with regional curves derived from aggregate site-discharge data). For all discharges, riffle morphological units (due to their shallow depth and high relative roughness) exhibited far greater diversity than pool units. All morphological features (except a plane bed) showed a significant increase in hydraulic biotope diversity as discharge increased from the lowest flow (Q_{92}) to intermediate discharges (around Q_{73}). Thereafter, overall biotope diversity was unchanging with further discharges increases up to the median discharge, though it tended to decrease markedly at high flows (Q_3).

Padmore (1997, 1998), in a more detailed study of relationships between flow exceedence percentiles and indices of both biotope patchiness (i.e. number of patches irrespective of type, for a given channel length of ten channel widths) and diversity (i.e. number of biotope units for a given channel length, multiplied by number of biotope types), based on transect-scale biotope classification for the 11 U.K. sites mentioned previously, also reported variability in the flow percentiles at which patchiness and diversity were maximised, with greater divergence in the latter index. For many sites, diversity and patchiness were greatest at moderate to low flows (between Q_{40} and Q_{100}), though diversity was lowered once discharges fell below Q_{95}. With flows above Q_{50}, as boundaries between biotopes became less distinct patchiness and diversity were reduced. Padmore (1997) deemed such results consistent with the generalisation that riverine habitat diversity is maximised at intermediate flows and decreases as discharges approach the extremes (Bain *et al*. 1988; Leonard and Orth 1988; Swales and Harris 1995). Interestingly, patchiness was greatest for low order streams of high flow and substratum heterogeneity, and diversity was maintained over a wider discharge range for such physically heterogeneous sites. That each site possessed a different patch-diversity signature suggested to Newson and Newson (2000) that some link was needed between the dynamics of mesoscale habitat patterns and channel geomorphological characteristics, a view supported by work in this thesis.

Habitat patch connectivity and refuge availability

The connectedness of flow or surface water patches within the river channel, or 'internal connectivity' (Uys and O'Keeffe 1997b) was a critical consideration in addressing low flow impacts on reach instream habitat. Reduction in water level affects not only the areal availability of suitable invertebrate habitat, but also the degree of habitat isolation, affecting the availability of refugia from the low-flow disturbance at a time of high vulnerability (Power *et al*. 1988; Section 1.4.3). In the present study, under natural low flow regimes changes in the extent of reach lateral and longitudinal connectivity were limited, with little bed exposure. Losses in patch connectivity became more pronounced as flows declined to extreme levels, however, with increased channel dissection leading to decreases in the number of flowing sections within the streambed (Sections 6.7.1-6.7.3), as well as increases in bed areas that were exposed, and partially or wholly desiccated with dewatering.

From an invertebrate perspective, it was clearly important to differentiate between and monitor both the overall reduction in suitable habitat and the flow-induced fragmentation that lead to progressively smaller and more isolated biotope patches within each reach (Section 1.4.6). The connectedness of biotopes as flow refugia is arguably as critical a factor as their hydraulic sensitivity to flow for invertebrate persistence under flow stress. In rivers, as for other systems, landscape connectivity (i.e. the spatial contagion of habitat) may be considered a threshold phenomenon, where fragmentation typically is not a linear function of habitat loss and even a minimal loss of habitat near a critical threshold is likely to disconnect the landscape, with possible consequences for population distributions and responses (Kotliar and Wiens 1990; With and Crist 1995; With *et al*. 1997). Whether or not the habitat fragmentation recorded in this study due to flow reduction impacted on the distribution of invertebrate populations was dependent in part on how taxa perceived or responded to the connectivity of the local landscape underlying the habitat patch mosaic (Taylor *et al.* 1993; With and Crist 1995; With *et al*. 1997). As With and Crist (1995, p. 2448) observed "Increasing habitat fragmentation may thus have little effect on species distributions until some critical level of connectivity is disrupted. It is not clear a priori where the critical threshold lies for species with different dispersal capabilities or habitat preferences". This raised the question whether in the context of the current study, during natural periods of low flow, conditions were still above a critical habitat connectivity threshold for all or most species, while with extreme flow reduction the degree of habitat fragmentation that occurred affected the majority of invertebrate taxa (see Chapters 7 and 8).

The structural heterogeneity of the river bed definitely proffered sources of protection from such flow-driven fragmentation (Lake 2000), with remnant stable or relatively hydraulically unaltered patches in the landscape potentially representing micro-scale refuges from flow disturbance (Scarsbrook and Townsend 1993). Where taxa associated with particular biotopes (Chapters 7 and 8) were unable to tolerate low flow conditions in a particular patch or migrate across physical barriers to other hydraulically tolerable patches, however, smaller-scale habitat elements potentially provided biologically critical refuges from localised disturbance (Power *et al*. 1988; Sedell *et al*. 1990; Kershner and Snider 1992). For instance, though small and temporary, areas of damp substratum and even refuges as small as the crevices of individual exposed stones had roles to play in invertebrate persistence over periods of extreme low flows (unpubl. data; Chapter 7).

6.7.4 Concluding remarks

Flow reduction led to consistent declines in the quantity and spatiotemporal availability of invertebrate hydraulic habitat, coupled with various changes in its hydraulic character, at reach, transect and individual patch scales, highlighting the importance of examining physical habitat within a spatially nested geomorphological hierarchy. Certain measures of hydraulic habitat were found to be more responsive and consistent in their degree and direction of response to flow reduction than others. Biotope patch metrics, which effectively encompass elements of both physical habitat quantity and hydraulic quality, were found to

be particularly useful and robust predictors of immediate effects of short-term low flow disturbance (as well as of invertebrate response – Chapters 7 and 8).

Even with natural discharge fluctuations, there were detectable changes in all physical habitat variables examined that created conditions less conducive for invertebrate persistence and could be considered at least mild disturbances, if only in the near-term. Abnormally low flows further reduced the overall living space for invertebrate assemblages, often well beyond the bounds of natural variability, with commensurate declines in the hydraulic quality and connectivity of the habitat patch mosaic - at least equally critical factors in terms of potentially adverse implications for invertebrates (Chapters 7 and 8). Even what appeared to be comparatively minor changes in available habitat due to discharge reduction might have potentially significant effects on biota. For example, although the habitat contraction associated with a 0.20 m water level decrease, with the natural shift from wet to dry seasons in a Panamanian stream, appeared insignificant at 18%, it resulted in a two- to four-fold decrease in critical deepwater refuges from predators for armoured catfish (Power *et al*. 1988).

Petts *et al.* (1995, p. 15) stated that "Our ability to predict biological responses, as opposed to habitat changes, remains weak (Armitage, 1994) but the objective assessment of habitat changes in relation to flow contributes valuable information to the decision-making process". The utility of the various flow-physical habitat relationships above, in identifying generalised and potentially meaningful low flow conditions for invertebrates, was conclusive. This author acknowledges, however, as have others (e.g. Wadeson 1996; Padmore 1997; Hollands 1998; Buffagni 2001), the primacy of demonstrable ecological responses to low flow disturbance in the latter regard (as explored in the next chapters).

7. DIRECT RESPONSES OF BENTHIC MACROINVERTEBRATE ASSEMBLAGES TO THE DYNAMICS OF LOW-FLOW DISTURBANCE

7.1 INTRODUCTION

7.1.1 State of research on invertebrate responses to low-flow disturbance

Comparatively few studies have examined the responses of riverine benthic macroinvertebrates to natural or unnatural, extreme low flows as critical disturbance events in space and over time (Tharme and King 1998; Lake 2000, 2003; Covich *et al*. 2003; Suren *et al*. 2003; Dewson *et al.* 2003, 2007c). Until recently, understanding of invertebrate assemblage responses to the effects of changing low flow regimes has also been disproportionately founded on broad or scattered studies, making it difficult to elucidate specific effects of flow events (Armitage 1995; Lake 2003) or identify truly generalised responses (Konrad *et al*. 2008). This lack of research investment is despite growing recognition in the realms of river ecosystem theory and management of the primacy of such flow disturbance events as determinants of benthos structure, spatiotemporal dynamics, and life-history strategies (Boulton and Suter 1986; Saltveit *et al*. 1987; Resh *et al.* 1988; Boulton *et al.* 1992b; Naiman *et al*. 2002; Lytle and Poff 2004; Section 1.4.3). Moreover, though it is generally agreed that a distinction is needed between the disturbance event itself and the responses of the biota to the event (Section 1.4.3; Lake 2003), there exist few cogent, ecologically relevant definitions of what constitutes a low flow event (though purely hydrological definitions exist - Smakhtin 2001). The terms that describe the vast array of potential low flow conditions, from natural and typically predictable shorter-term low flows or seasonal droughts to which the biota are adjusted (Boulton 2003), through to abnormally reduced flows and supra-seasonal droughts, remain loosely employed (Gordon *et al.* 1992; Lake 2000, 2003; Humphries and Baldwin 2003; Dahm *et al*. 2003). In the context of the current study, manipulated low flows have been defined as 'extreme' in terms of elements of flow regime variability and predictability outside those typifying natural dry-season low flows (Humphries and Baldwin 2003; Lake 2003; Section 1.4 and Chapter 4).

Without doubt, a great deal has been learnt about the effects of low flow as a physical disturbance on invertebrates from studies of floods (Section 1.4.3), although the two kinds of event differ with respect to the physical and chemical stresses they exert on biota, as well as in relation to the duration, return period and spatial extent of impact (Humphries and Baldwin 2003). For example, substratum movement, while adopted as a central measure of flood disturbance intensity (McElravy *et al*. 1989; Rader and Ward 1989; Death and Winterbourn 1994; Death 1996a; Downes *et al*. 1998a; Townsend *et al*. 1997a, b) holds little immediate

relevance at low flows. Flood studies have cast light on varied responses of invertebrate assemblages and species populations, in terms of changes in distribution, composition and behaviour patterns, during and after flow events of differing disturbance characteristics (Gray 1981; Gray and Fisher 1981; Meffe and Minckley 1987; Scrimgeour *et al*. 1988; Palmer *et al*. 1992; Boulton and Lake 1992b). They have proved especially insightful in cases where flow disturbance regimes and invertebrate dynamics have been rigorously characterized at multiple spatial and temporal patch scales (e.g. Fisher *et al.* 1982; Scarsbrook and Townsend 1993; Death and Winterbourn 1994, 1995; Townsend *et al*. 1997a, b; Boulton 2003; Silver *et al*. 2004), and for multiple events (e.g. Grimm and Fisher 1989). Simulated physical disturbances of the streambed, often to mimic flood effects and occasionally combined with same-river studies of natural flow-mediated disturbance (e.g. Boulton *et al.* 1988; Doeg *et al*. 1989; Lake *et al.* 1989; Death 1996a, b; Matthaei *et al*. 1997; McCabe and Gotelli 2000), while subject to limitations (Matthaei *et al.* 1997) and less useful for understanding low flow responses *per se*, also have served to advance flow disturbance theory. For instance, in New Zealand, the effects of disturbance history on invertebrate recovery from experimental, small-scale disturbance of streambed patches in two hydrologically variable streams were compared with those on two more stable systems (Death 1996b). Matthaei *et al*. (1997) documented recovery responses of various benthic invertebrate taxa to both natural and experimental flood disturbances in the Swiss River Necker.

Despite being an ecologically vital counterpart to floods, low-flow disturbances, from a reduction in the amount of flow through to the total loss of surface water and connectivity, have received lesser attention (Boulton and Suter 1986; Stanley and Fisher 1992; Lake 2003) such that their impacts on stream habitats and biota remain quite poorly understood (Lake 2000). Indeed, Suren *et al*. (2003, p. 71) stated that "Very little is known of invertebrate responses to natural or artificially induced low flows, and how community composition may change during summer as flows decrease." Most studies of the ecological effects of low-flow perturbations, a few from some fifty years ago (Stehr and Branson 1938; Hynes 1958; Larimore *et al.* 1959; Kamler and Riedel 1960) have been opportunistic, descriptive, and often at small spatial and short temporal scales (Lake 2000, 2003). As such, they are considered limited in the extent to which they are able to "disentangle the relative effects of the spatial from the temporal extent of low flows and of these from the pattern of drying of the river bed" (Humphries and Baldwin 2003, p. 1144).

Much of the body of literature on effects of low flows on invertebrates has been devoted to a few avenues of investigation, relatively seldom focused on perennial rivers where extreme low flows and drying might be expected to be infrequent and less predictable than for temporary systems (Ledger and Hildrew 2001; Lake 2003; Suren *et al*. 2003; Dewson *et al.* 2007c). While a wealth of fundamental knowledge has been gleaned from studies of the impacts of flow regime regulation by impoundment on invertebrate assemblages of perennial rivers (see Section 1.3.3), isolation of the influences of specific low flows from other confounding disturbance effects has often proved complex. Substantial information also exists in the form of phenomenological accounts of the impacts of drought and associated flow state changes (Townsend 1989) or surprisingly less commonly, normal dry-season flows, on the invertebrate fauna of variously temporary or

perennial rivers (Larimore *et al*. 1959; Harrison 1966; Iversen *et al.* 1978; Ladle and Bass 1981; Resh 1982; Taylor 1983; Canton *et al*. 1984; Cowx *et al.* 1984; Kownacki 1985; Wright and Berrie 1987; Chessman and Robinson 1987; McElravy *et al.* 1989; Cuffney and Wallace 1989; Morrison 1990; Bickerton *et al.* 1993; Miller and Golladay 1996; Pollard *et al.* 1996; Ledger and Hildrew 2001; Suren *et al*. 2003; Covich *et al*. 2003). Other studies have actively investigated the biophysical effects of flow reduction and intermittency, commonly in naturally temporary rivers of differing flow permanence and variability (Boulton and Suter 1986; Delucchi 1988, 1989; Boulton and Lake 1988, 1990, 1992a, b; Bottorff and Knight 1988; Boulton *et al.* 1992a, b; Boulton and Stanley 1995; Williams 1996; Feminella 1996; Stanley *et al.* 1997; Uys and O'Keeffe 1997a, b; O'Keeffe and Uys 1998). Insights from these studies are germane for perennial rivers, especially where comparative studies have demonstrated considerable structural and functional overlap of temporary and permanent invertebrate faunas (*sensu* Williams and Hynes 1977), such that there is reason to expect some similarities in low flow responses (Boulton and Suter 1986; Bottorff and Knight 1988; Delucchi 1988; Boulton and Lake 1992a; Miller and Golladay 1996; Feminella 1996; O'Keeffe and Uys 1998).

Though artificial manipulation of flows at appropriate scales is difficult (Townsend 1989), a few field-based experiments of the effects of discharge reduction on invertebrates of permanent rivers have been conducted, typically fairly short-term and for small systems (Hooper and Ottey 1988; Poff and Ward 1991; Tharme and King 1998; Dewson *et al*. 2007a, b; James *et al*. 2008, 2009). Although subject to these limitations, in most such experiments, including the present one, baseline low flow responses for the natural dry season or pre-impact controls have been established (Boulton 2003; Section 3.1). Several studies of the effects of existing water diversions exist, for comparison with such experiments (Dudgeon 1992b; Castella *et al*. 1995; Rader and Belish 1999; McIntosh *et al*. 2002, 2008; Dewson *et al*. 2003). Invertebrate responses to the effects of manipulated and natural flow reductions often appear similar (Tharme and King 1998; McIntosh *et al*. 2002; Dewson *et al*. 2007c).

7.1.2 The nature of low-flow disturbance

Effects of low flows on invertebrate assemblages and their responses can usefully be considered across a continuum of shifting hydrologic phases, as outlined in Stanley and Fisher (1992, p. 272, Figure 1) and Lake (2000; Section 6.1.1, Figure 6.1). While the former conceptual framework focused on partitioning drying disturbance and recovery at low flows in intermittent streams, it is still pertinent for perennial systems, particularly if re-examined with a patch dynamics perspective or along a flow permanency gradient. Low flow phases essentially encompass: at the onset, reduced flow volume, discharge and water level; then flow cessation and development of intermittent conditions; complete loss of surface water; streambed desiccation; and ultimately, rewetting with flow resumption. The progressive habitat shrinking that results in altered hydraulics, fragmentation and patch boundary collapse (Fisher and Grimm 1991; Stanley *et al*. 1997; Boulton 2003) may continue until aquatic habitat is entirely lost and spatial intermittency extends beyond the reach (Lake 2003; Section 6.1).

The direct perturbation effects of low flows on the benthos centre on this loss of water, habitat, and thus, dispersal routes for organisms (Lake 2003), with the ecological consequences of loss of flow or surface water obviously different from the effects of altered flow volumes, but not necessarily more severe (Uys and O'Keeffe 1997b). Each hydrologic phase variously influences the distributions and abundances of individual taxa within an assemblage over time (Boulton and Suter 1986; Boulton and Lake 1990, 1992a; Stanley and Fisher 1992; Uys and O'Keeffe 1997a), likely in a stepped manner (Yount and Niemi 1990; Lake 2000; Boulton 2003, p. 1176, Figure 1). Critical stages when conditions might rapidly become unfavourable, such as with habitat isolation or loss, are then defined by specific thresholds in water level or discharge. Organisms may persist under such flow state changes by tolerance, avoidance, or both responses (Clinton *et al*. 1996; Lake 2003; Boulton 2003), potentially also experiencing life cycle disruption or death. Less is known about the biological effects of the timing and rapidity of hydrological transitions across low flow states and thresholds, than of individual states (Boulton 2003). Further, as low-flow disturbances are not uniform in characteristics such as their magnitude, extent of influence or duration, they do not affect taxa in the same way in the short- or long-term (Connell and Sousa 1983; Pickett and White 1985; Grimm 1994; Lake 2003; Section 1.4.3), contributing to a diversity of assemblage responses (Section 7.1.3). Generally, more extreme disturbances (e.g. unpredictable timing, protracted duration, multiple events) induce more profound and enduring invertebrate responses (Canton *et al*. 1984; Cowx *et al.* 1984; Delucchi 1988; Jowett 2000; O'Keeffe *et al*. 2002; Suren *et al.* 2003; Boulton 2003). Impacts may be disproportionately severe when critical thresholds are exceeded (Larimore *et al*. 1959; Boulton 2003).

Invertebrate responses are obviously further complicated by contributing factors that also vary with the flow disturbance event (Death 1996b), in addition to the dynamics of flow and physical habitat, notably altered water chemistry, food and other resources (Sections 1.4.6 and 5.1). Other sources of influence include the degree to which life history attributes of species enable them to withstand low flow stresses, the intensity of interactions among organisms, and ecosystem properties such as stability (Stanley and Fisher 1992; Death and Winterbourn 1994; Death *et al*. 2009). It was not the intent in this thesis to explicitly address life history traits (multiple generations, short development times, diapauses, etc.), behaviour patterns, or morphological and physiological specialisations. Their importance in being modified by the prevailing hydrological regime (Lake *et al.* 1985; Poff and Ward 1989; Walker *et al.* 1995; Miller and Golladay 1996; Bunn and Arthington 2002; Lytle and Poff 2004) and thus, shaping even short-term invertebrate response to and strategies for persistence with low-flow disturbance (e.g. Larimore *et al.* 1959; Harrison 1966; Williams and Hynes 1977; Iversen *et al.* 1978; Gray 1981; Fisher *et al*. 1982; Cowx *et al.* 1984; Canton *et al*. 1984; Perry and Perry 1986; Brittain and Saltveit 1989; Morrison 1990; Yount and Niemi 1990; Feminella 1996; Williams 1996; O'Keeffe and Uys 1998; O'Keeffe and Dickens 2000; Boulton 2003) is paramount, however, and acknowledged here. Flow disturbance history, or the legacy of flow regime variability and antecedent flow conditions, is also a vital factor often overlooked (Wright *et al.* 1984; Perry and Perry 1986; Brittain and Saltveit 1989; Stanley and Fisher 1992; Tharme and King 1998; Lake 2000; Boulton 2003; Konrad *et al*. 2008; Sections 1.4.4 and 4.1).

Many studies of low flows have neglected, assumed rather than quantitatively examined, or been unable to adequately tie invertebrate responses to such diverse interconnected factors, which while adverse for some taxa might be favourable for others. In this thesis, an attempt is made to partly redress this in relating direct invertebrate responses to concomitant changes in habitat availability and quality, across ecologically meaningful patch scales, as well as to the flow disturbance regimes characteristic of each study river (Section 1.2).

7.1.3 An overview of effects of flow reduction and extreme low flows on invertebrates

Various direct (and indirect) responses to flow reduction and severe low flows have been recorded for benthic invertebrate taxa, leading to diverse outcomes for entire assemblages, often in response to the same flow disturbance or for similar rivers (Tharme and King 1998, McIntosh *et al*. 2002, 2008; Dewson *et al.* 2007c). Authors have reported increases, decreases, or no detectable change in response metrics that span patterns of trophic structure, assemblage distribution and composition, taxon richness, abundance and other diversity indices, behaviour, physiology and other life history attributes. While the overwhelming diversity of responses, especially when coupled with broader biogeographic considerations (Castella *et al*. 1995; Dewson *et al*. 2003; Poff *et al.* 2006a; Monk *et al.* 2006; Konrad *et al*. 2008), may render it difficult to extract general trends, it highlights well the range of response options open to benthic invertebrates, as well as the particular challenges each poses.

Stranding and exposure with flow reduction

Invertebrate survival during flow reduction and drying requires an ability to keep pace with shrinking stream margins and wetted area. Conditions can be severe during the phase when water is absent (Boulton 1989, 2003; Stanley and Fisher 1992; Boulton *et al.* 1992a), when epigean biota must rely on behavioural and/or physiological strategies to avoid desiccation and persist. Exposure, particularly in shallow marginal habitats and even for short periods, can result in devastating effects on benthic invertebrates, including mortality and subsequent declines in productivity (Larimore *et al.* 1959; Iversen *et al.* 1978; Extence 1981; Weisberg *et al.* 1990). Many invertebrate taxa are, however, clearly able to survive short duration extreme low flows and streambed desiccation.

The risk and degree of invertebrate stranding with reduced flows differ according to not only the magnitude and rate of flow change, but also season, temperature, degree and frequency of streambed dewatering, and antecedent conditions (Pearson and Franklin 1968; Fisher and LaVoy 1972; Kroger 1973; Corrarino and Brusven 1983; Perry and Perry 1986). Intrinsic biotic attributes including relative vagility, taxon flow sensitivities, and physiological adaptations, also influence the nature of response (Pearson and Franklin 1968; Fisher and LaVoy 1972; Extence 1981; Car 1983; Corrarino and Brusven 1983; Perry and Perry 1986). Some species are particularly susceptible to stranding, due to difficulties in movement during substratum desiccation, or because they are sessile or less mobile than other taxa (Cushman 1985). With discharge

declines below Flaming Gorge Dam, U.S.A., which exposed 25% of the previously wetted Green River bed, most *Baetis* nymphs avoided stranding by crawling or occasionally swimming towards deeper water (Pearson and Franklin 1968). Simuliid larvae less successfully avoided receding water levels, and were common dead or alive under exposed substrata. Although an immediate six-fold drift of predominantly *Simulium chutteri* larvae (as well as Chironomidae, Ephemeroptera, Trichoptera) occurred in response to a manipulated 54% water level reduction in the South African Orange River, large simuliids that could not easily remain in the drift were stranded and starved in non-flowing pools (Car 1983). With gradual declines in water levels or wetted habitat, as mostly occur with natural flow reductions, however, there is usually time for a high proportion of the benthos to relocate to more suitable areas (e.g. Moon 1956; Extence 1981; Corrarino and Brusven 1983; Jensen and Jensen 1984; Cushman 1985; McIntosh *et al*. 2002, 2008; Dewson *et al*. 2007a, b). The majority of, but not all, taxa avoided stranding with extreme flow reduction during drought in the perennial River Roding, U.K. (Extence 1981). The pulmonate snail, *Lymnaea peregra*, for instance, was never observed stranded on exposure and increased in abundance, in contrast to its prosobranch counterparts, because it is more mobile and physiologically better adapted to survive stranding.

With severe and/or unnaturally rapid discharge reductions (e.g. peaking hydropower), although not only in such circumstances, major stranding and oftentimes high mortalities are more common (Pearson and Franklin 1968; Fisher and LaVoy 1972; Kroger 1973; Brusven *et al*. 1975; Corrarino and Brusven 1983; Cushman 1985; Perry and Perry 1986; Weisberg *et al.* 1990; Bretschko and Moog 1990). Experimental discharge manipulations in the regulated Flathead and Kootenai rivers, U.S.A., resulted in greater invertebrate stranding with a faster rate of decrease in discharge (Perry and Perry 1986). Flow reduction subsequent to extended periods of more constant discharge in the Kootenai River, which briefly provided more stable conditions, also produced more extreme stranding than flow reductions after periods of frequently fluctuating flows. Considerable numbers of riffle taxa were affected, including *Simulium* spp., Chironomidae, *Ephemerella inermis*, and *Baetis tricaudatus*. Stranding of all riffle invertebrates, massive mortalities, and elimination of flow-sensitive stoneflies and several other taxa, occurred due to a rapid discharge decline and associated 0.30 m decrease in water levels that exposed large riverbed areas in the Snake River, U.S.A. (Kroger 1973). Differential summer stranding of benthic invertebrates occurred in shallow marginal areas downstream of a dam on the Connecticut River, U.S.A., depending on whether the riverbed was exposed 70%, 40%, 13%, or none of the time with major flow reduction (Fisher and LaVoy 1972). Assemblages exposed only 13% of the time did not differ significantly from those in areas always submerged, suggesting the benthos tolerated brief periods of bed exposure. In contrast, assemblages within areas more frequently exposed were of markedly altered composition than those continuously submerged, with a loss of flow sensitive Ephemeroptera and Trichoptera to the advantage of more tolerant chironomids and oligochaetes.

Some stranded individuals become a food source for terrestrial and aquatic predators or scavengers. Moon (1956) attributed the presence of carnivorous flies, in areas of exposed wet mud with natural, very low flows

and drying in a small Chalk stream, to increased availability of exposed aquatic larvae as food. Predation by terrestrial beetles was elevated with drought in the largely perennial Smiths Branch Stream, U.S.A. (Larimore *et al*. 1959). A wide diversity of predatory and scavenging terrestrial insects intimately associated with the stream environment were observed feeding on stranded dead and dying aquatic invertebrates during drying in an intermittent stream (Stehr and Branson 1938).

Drift responses with flow reduction

Drift has been well established as a mechanism by which invertebrates redistribute typically very short distances downstream in low numbers at natural flows, as well as in response to unfavourable conditions (Corkum *et al*. 1977; Perry and Perry 1986; Brittain and Eikland 1988; Poff and Ward 1991; Dewson *et al.* 2007c; Section 1.4.3). Some invertebrates have altered their time in the water column during a single drift event depending on flow regime (Minshall and Winger 1968; Poff and Ward 1991). Numerous observational and experimental studies have shown increased invertebrate drift with flow increases and floods (Pearson and Franklin 1968; Anderson and Lehmkuhl 1968; Armitage 1977; Corkum *et al.* 1977; Scullion and Sinton 1983; Corrarino and Brusven 1983; Perry and Perry 1986; Hooper and Ottey 1988; Brittain and Eikeland 1988; Layzer *et al.* 1989; Poff and Ward 1991; Imbert and Perry 2000). Similarly, discharge-drift relationships, typically taxon-specific and sometimes consistent across seasons (Poff and Ward 1991), are well established with flow reduction (Minshall and Winger 1968; Armitage 1977; Gore 1977; Car 1983; Corrarino and Brusven 1983; Canton *et al.* 1984; Hooper and Ottey 1988; Poff and Ward 1991; James *et al.* 2008, 2009). Several supporting studies are liable to be of lesser relevance than others in this thesis context, however, as they addressed the effects of severe and rapid discharge reversals with hydropower operation (e.g. Pearson and Franklin 1968; Radford and Hartland-Rowe 1971; Perry and Perry 1986). Additionally, experimental research was sometimes potentially confounded by sequentially introducing different flow events, such that organism responses to individual events were not necessarily independent (e.g. Hooper and Ottey 1988; Poff and Ward 1991).

Most commonly, flow reduction has induced increased invertebrate drift densities and/or rates (Minshall and Winger 1968; Corkum *et al.* 1977; Corrarino and Brusven 1983; Canton *et al*. 1984; Poff and Ward 1991; James *et al.* 2008, 2009). Poff and Ward (1991) reported that the drift responses of several taxa were stronger with reduced discharge than elevated flows. Responses may be immediate or delayed, and with diel differences (Pearson and Franklin 1968; Corrarino and Brusven 1983; Perry and Perry 1986; Brittain and Eikeland 1988; Poff and Ward 1991). Decreases in drift by invertebrate taxa with flow reduction are less commonly encountered (Minshall and Winger 1968; Poff and Ward 1991). In some instances, no change or inconsistent drift responses have been reported in response to flow reduction (Poff and Ward 1991; James *et al.* 2008). Poff and Ward (1991) postulated that active drift entry (behavioural abandonment of the substratum), as compared with passive displacement, was probably a contributor to altered drift densities at reduced flows, particularly for taxa that are naturally able to maintain position hydrodynamically or swim well at low velocities. Moreover, while interactions between individuals at subsaturation densities may

result in short-distance displacements, but seldom in drift, density-dependent drift may occur once density exceeds available substratum space (Ciborowski 1983). Importantly, extremely low flows and flow cessation are considered to inhibit drift as a major means of invertebrate redistribution or recolonisation (Boulton 2003; Dewson *et al.* 2007c; James *et al.* 2008, 2009).

With artificial discharge diversion in the regulated upper Colorado River, U.S.A., the majority of riffle invertebrate taxa (e.g. *Baetis* spp., *Epeorus longimanus*, Simuliidae; *Isoperla* sp.) showed the same response trend with elevated drift densities and rates, as compared with established patterns at natural low flows during and before manipulation (Poff and Ward 1991). Drift rates declined for some other taxa (e.g. *Ephemerella infrequens*, *Lepidostoma ormea*) or showed no change. A few taxa varied in both the timing and direction of their response to discharge reduction or modified their daily drift patterns with flow reduction (e.g. *Paraleptophlebia heteronea*, *Triznaka signata*). Changes in hydraulic habitat were considered the probable flow-mediated contributors to altered drift patterns, as dissolved oxygen and seston levels were unchanged. The same trends in drift responses were evident for riffle assemblages with experimental streamflow reductions of more than 89% for one-month, in three New Zealand streams (James *et al.* 2008). A sustained increase in drift propensity at Booths Creek was found for total number of individuals. Typically, grazers and deposit feeders (e.g. Orthocladiinae) also showed increases in drift throughout the period of reduced flows rather than a fairly rapid return to pre-reduction levels, probably because of increased abundances or levels of activity over a wider area of suitable habitat. Immediate, but short duration drift increases in the total number of drifting individuals, as well as taxa such as *Austrosimulium*, the leptophlebiid, *Austroclima sepia*, and baetids, occurred in Kiriwhakapapa Stream and Reef Creek. Certain taxa showed a lack of drift response or an inconsistent response, including another leptophlebiid, *Deleatidium* sp., as well as hydroptilid, philopotamid and plecopteran species. Drift composition was broadly similar to that of the benthos, though a few taxa were disproportionately more (e.g. simuliids, chironomids) or less (gastropods) prevalent in the drift. Differences in drift propensities were posited to be due to changes in riffle habitat and preferred velocities, ability to maintain contact with the substratum, as well as possibly intensified biotic interactions under increased benthic densities (James *et al.* 2008, 2009).

In the above studies, and many others of low flows, drift was linked to declines in physical habitat availability and suitability, by implication or explicitly. A strong negative relationship between discharge and invertebrate drift density in summer in Maize Beck, U.K., with the highest concentrations of benthos in the drift recorded during low discharges, was presumed due to reduced wetted habitat (Armitage 1977). Increased benthic crowding, due to reduced wetted width and depth, was considered a likely cause of exceptionally high drift displacement of invertebrates, predominantly ephemeropterans, with streamflow reduction in the Kananaskis River, Canada (Radford and Hartland-Rowe 1971). High (nocturnal) drift rates following drastic daytime flow reductions on the Green River, USA, below Flaming Gorge Dam, were attributed to *c.* 25% streambed exposure, coupled with high total benthic density (Pearson and Franklin

1968). The most responsive taxa were baetid mayflies, stoneflies and trichopterans, while Simuliidae larvae increased only slightly in the drift. Massive daytime increases in invertebrate drift density (cf. controls) were demonstrated in artificial channels on Grande Ronde River, U.S.A., with experimental flow reductions (Corrarino and Brusven 1983). Initial flow reduction reduced wetted perimeter by 8%, leading to a minor drift increase, but further flow reduction exposed 31% of the bed, generating a short-term increase in benthic densities that triggered catastrophic drift of a high diversity of taxa.

The propensity of certain invertebrates to enter the drift at low flows is often directly in response to altered hydraulics, particularly decreased current velocities (e.g. when physiological or dietary needs cannot be met, or biotic interactions intensify) (Minshall and Winger 1968; Ciborowski *et al.* 1977; Corrarino and Brusven 1983). Experimentally it was shown that drift of rheophilic *Baetis vagans* nymphs increased at very low velocities and *B. tricaudatus* were more prone to leave the substratum under low than high velocities (Corkum *et al*. 1977). Drift was benthic density-independent, but positively proportional to current velocity for two mayfly species, with *Ephemerella inermis* exhibiting a propensity to drift at experimental velocities both higher and lower than preferred values (Ciborowski 1983). A major drift increase for most taxa represented in the benthos, in response to two discharge reductions due to experimental diversion and associated declines in velocity and depth, occurred in a small stream, Spring Run Creek, U.S.A. (Minshall and Winger 1968). There were no definitive relationships between changes in either velocity or depth and taxon drift, but increases in drift numbers appeared proportional to velocity reduction. Drifting taxa intolerant of low flows and associated velocities included ephemeropterans, *Simulium,* Chironomidae, oligochaetes, a stonefly, trichopterans and, unusually, *Dugesia*. A few taxa showed reduced drift numbers with progressive flow reduction, including the cased caddis, *Neothremna*, which was presumed unable to enter the drift when the velocity was too low to transport it.

Different degrees and sequences of discharge reduction, and patterns of antecedent flows, can result in progressively stronger, weaker or otherwise altered (e.g. diurnal vs. nocturnal) drift responses. James *et al.* (2008, p. 32) found that "taxa are responding to some threshold of flow and not just change in flow *per se*" in a study of the effects of one-month long experimental flow reductions on macroinvertebrate drift in experimental streamside channels adjoining Mayfly Creek, Canada. Increased drift densities occurred, especially for *Baetis*, and with similar response patterns observed for Tanypodinae and a trichopteran, where discharge was reduced by 75%, but not by 50%, from control discharge levels. The flow reductions did not trigger drift responses for Orthocladiinae or Oligochaeta. Dramatic increases in invertebrate drift occurred in the flow-regulated Tongue River, U.S.A., with 30% discharge reduction and massive drift with a further 10% reduction (Gore 1977). Different discharge events (viz. drought, normal, high) manipulated in various day-night sequences following summer control periods, resulted in complex patterns of drift response by various riffle invertebrate taxa (and changes in benthic assemblage composition), in two sets of biophysically dissimilar experimental stream channels in Convict and Hunt creeks, U.S.A. (Hooper and Ottey 1988). Flow disturbance experiments in the Flathead and Kootenai rivers indicated that antecedent flow characteristics

were important in governing drift response with discharge reduction (Perry and Perry 1986). Flow reduction after long periods of more stable conditions in the Kootenai R. generated more extreme drift than after periods of variable flows. In part because invertebrate populations were adjusted to a more frequent flow-disturbance history, drift responses in the flow-variable Flathead R. were less pronounced with discharge reduction.

Changes in invertebrate assemblage composition and diversity with low flows

Low flows, whether representing naturally or artificially severe events, typically elicit detectable, if not significant, changes in benthic assemblage composition and diversity (Dewson *et al.* 2007c); assemblage shifts similarly occur with elevated discharges (e.g. Snaddon and Davies 1998). The directions and degrees of response are liable to depend on the initial mix of species comprising the assemblage, given the wide range of taxon-specific habitat and life cycle requirements (Ward 1976; Iversen *et al.* 1978; Dewson *et al*. 2007a, c; James *et al.* 2009; this study), and potential for biotic interactions. Physical habitat reduction and altered local environmental conditions, as well as the form, degree and gradient of flow disturbance, constitute other basic elements influencing response. It is perhaps unsurprising therefore, that a wide range of low flow studies have yielded such a disparate array of assemblage-level changes in invertebrate composition within a single reach and its mesohabitats, or across rivers of similar or different types, as illustrated below (see also Section 7.8).

Increases and/or decreases in the total abundances of invertebrates, as well as in the densities of specific benthic components, are the most widely reported responses to natural and unnatural reductions in discharge, oftentimes in the same river. Reductions in densities are common (Hynes 1958; Larimore *et al.* 1959; Iversen *et al.* 1978; Ladle and Bass 1981; Extence 1981; Canton *et al.* 1984; Cowx *et al.* 1984; Wright and Berrie 1987; Chessman and Robinson 1987; Hooper and Ottey 1988; Delucchi 1988; Dudgeon 1992b; Wood and Petts 1994, 1999; Castella *et al.* 1995; Pollard *et al.* 1996; Weeks *et al.* 1996; Rader and Belish 1999; Cazaubon and Giudicelli 1999; Ledger and Hildrew 2001; McIntosh *et al*. 2002, 2008; Suren *et al.* 2003). Increases in total abundance or individual taxon densities with low flows have also been documented (Gore 1977; Ladle and Bass 1981; Extence 1981; Canton *et al.* 1984; Wright and Berrie 1987; Armitage and Petts 1992; Dudgeon 1992b; Castella *et al.* 1995; Pollard *et al.* 1996; Rader and Belish 1999; Ledger and Hildrew 2001; Suren *et al.* 2003; Dewson *et al.* 2003, 2007b). In other instances, also sometimes within the same river, decreased streamflows did not elicit a discernible change from natural in either overall or taxon-specific abundances (Iversen *et al.* 1978; Ladle and Bass 1981; Canton *et al.* 1984; Chessman and Robinson 1987; Cuffney and Wallace 1989; Dudgeon 1992b; Castella *et al.* 1995; Armitage and Pardo 1995; Englund and Malmqvist 1996; Rader and Belish 1999; Wood *et al.* 1999; Caruso 2002; Suren *et al.* 2003; Dewson *et al.* 2003, 2007a, b; McIntosh *et al*. 2008).

In terms of invertebrate richness, Shannon-Weiner diversity and other diversity measures, low-flow disturbances have most commonly decreased diversity in the short- and longer-term, frequently with

localised losses in specific taxa (Hynes 1958; Larimore *et al*. 1959; Ward 1976; Iversen *et al*. 1978; Extence 1981; Wright and Berrie 1987; Chessman and Robinson 1987; Hooper and Ottey 1988; Delucchi 1988; Dudgeon 1992b; Boulton and Lake 1992b; Wood and Petts 1994, 1999; Bickerton 1995; Pollard *et al*. 1996; O'Keeffe and Uys 1998; Cazaubon and Giudicelli 1999; Rader and Belish 1999; Wood *et al*. 1999; Davies *et al*. 2000; Caruso 2000; Ledger and Hildrew 2001; McIntosh *et al*. 2002, 2008; Suren *et al.* 2003; Dewson *et al.* 2003, 2007a). The declines in richness and diversity might not only be apparent overall, but also in relation to habitat type, and frequently in instances where surface flow ceased and habitat diversity diminished (Dewson 2007c). In fewer instances, decreasing flows have been reported to increase (Hooper and Ottey 1982; Bickerton 1995; Dewson *et al.* 2003) or have no detectable or consistent effect on taxon richness and similar biotic measures (Chessman and Robinson 1987; Bickerton 1995; Castella *et al.* 1995; Armitage and Pardo 1995; Englund and Malmqvist 1996; Rader and Belish 1999; Choy *et al.* 2000; Suren *et al.* 2003; Dewson *et al.* 2003, 2007a, b).

Studies involving manipulated low flows similar to the present one have had varying effects on invertebrate composition (as discussed further in Section 7.8.1). Experimental flow reduction in U.S. Convict Creek resulted in the restructuring of riffle benthic assemblages and marked decreases in the abundances of several key species; there was no attempt to correlate response with reported physical habitat change (Hooper and Ottey 1988). Conversely, total riffle densities consistently increased, though not significantly and by variable proportions, in three New Zealand streams affected by short-term artificial discharge reductions of, on average 89-98%, over one dry-season month (Dewson *et al*. 2007b). This was despite commensurate drift increases immediately following flow reduction (James *et al.* 2008, 2009). The most common taxa in each stream also increased in density at very low discharges, with no taxa eliminated. The number of riffle taxa, proportion of Ephemeroptera, Plecoptera and Trichoptera (% EPT), riffle species evenness, and Quantitative Macroinvertebrate Community Index were unchanged. With similar magnitude artificial flow reductions, but for two months to a year in the same streams, responses were consistent for the few taxa shared, whether increases, decreases or no change in densities (Dewson *et al*. 2007a, b; Death *et al*. 2009). Although Simpson's diversity did not change in response to short-term or protracted low flows in any of the streams, other measures of riffle assemblage composition declined in the near-natural Reef Creek with two months of severe flow reduction, as did the densities of several dominant species. In the slightly anthropogenically impaired Kiriwhakapapa Stream, taxon richness decreased in the second month of low flows, and decreased densities of common flow-sensitive taxa were major contributors to the divergence of flow-impacted and unimpacted riffle assemblages. In the polluted Booths Creek, the only obvious response was a decrease in the abundance of one mayfly species.

Downstream of a water diversion abstracting 92-97% of summer daily discharge on the upper reaches of perennial Iao Stream, Hawaii, mean total density and diversity of riffle communities were significantly reduced, with the former measure 46% greater at natural low flows (McIntosh *et al*. 2002). Effects on rheophilic taxa were particularly obvious, and although the numerically dominant taxa remained relatively

consistent in their relative abundances at natural and severely reduced flows, mean densities were significantly higher in the undisturbed reach for Chironomidae, Hydroptilidae, dipteran pupae, and a group that included Oligochaeta. The sole dominant riffle group unaffected was Trichopteran pupae. Shifts in composition in non-dominant taxa also occurred. Major diversion of 98% of dry-season baseflow for water supply in the perennial upper Waihee River, Hawaii (a larger stream, also with a naturally highly variable flow regime), conversely did not lead to a significant change from natural in riffle total density, although densities varied temporally across individual months (McIntosh *et al*. 2008). Density was 29% lower in the flow-disturbed reach, however, and the mean total biomass of three major families combined was reduced by 60%. Abundances were significantly lower than natural for a few flow-sensitive taxa, while many others showed little response regardless of altered physical habitat. A few taxa were locally eliminated (as also occurred in Iao Stream). While it was impossible to discern trends in total population densities of riffle invertebrates with streamflow diversion in a perennial reach of Tai Po Kau Forest Stream, Hong Kong, due to their marked fluctuations immediately before flow cessation and during winter low flows, richness declined conspicuously after surface flow diminished and the upper streambed desiccated (Dudgeon 1992b). It reached lowest levels at the end of both dry seasons studied. Individual taxa showed marked increases (e.g. *Helodes* sp.) or, more commonly, decreases in density (e.g. Trichoptera), with clear differences in relative flow sensitivity.

Dependent on whether baseflow diversion for water supply was mild or severe in three small, perennial Rocky Mountain streams, U.S.A., responses in terms of riffle invertebrate composition differed over one year (Rader and Belish 1999); recovery was rapid with the onset of higher flows in all cases. Minor baseflow diversion (25%, with no dewatering and retention of a natural flow pattern) in St. Louis Creek did not reduce invertebrate abundance or taxon richness from that of unimpacted assemblages upstream. Five months of higher (40%) constant diversion led to markedly increased densities, and for all taxa. In contrast, discharge reduction of almost 100% for about 11 months, in a tributary, West St. Louis Creek, reduced total invertebrate density and species richness, as compared with controls. Chironomidae were favoured by the extreme flows, but most taxa, notably Ephemeroptera, declined or were locally extirpated. Similar trends were reported for the totally diverted East St. Louis Creek. Irrespective of differing magnitude flow reductions (28-98%) across four N.Z. streams that differed from one another in location and invertebrate composition (flow regime type was not assessed), for riffle invertebrate communities sampled once upstream and downstream of existing abstraction points, none of eight invertebrate metrics showed a consistent response (Dewson *et al*. 2003). Significant differences in riffle communities in reaches below abstraction points from those upstream were typically a function of increased average taxon abundances with flow reduction, although decreases also took place (e.g. *Austrosimulium* sp.). No common taxa were lost or gained due to flow reductions, but 11 rare taxa that included members of the Plecoptera, Ephemeroptera, Tanypodinae and Trichoptera were restricted to one or more sites above offtakes. Moreover, three other uncommon taxa were unique to flow-disturbed reaches. Changes in invertebrate composition were generally limited and inconsistent across groups of rivers of similar biophysical type from within 22 different streams

across the U.K. subjected to a broader array of different kinds and degrees of water abstraction, with paired reference and impacted sites (Castella *et al*. 1995). Minor diversions tended to result in lesser disturbance responses than moderate or major ones, however, and certain families were demonstrably more low-flow sensitive than others. For the regime type of groundwater-dominated lowland rivers, such as the Wissey, some consistency in invertebrate response was detected for a diverse group of families that decreased in abundance with flow reduction and associated hydraulic changes. Across many sites on 22 British rivers that reflected a diverse range of biophysical types and water abstraction effects, invertebrate abundance was a more sensitive and consistent indicator of flow-related change than number of taxa or River Invertebrate Prediction and Classification System, RIVPACS, biotic score (Armitage and Petts 1992). The lack of adverse effects of flow reduction typically observed for upland streams, as compared with lowland sites, was attributed to the greater flow variability and hydraulic habitat heterogeneity of the former sites, with their fauna possibly well adapted to extreme conditions involving wetted habitat loss.

Differences in responses to natural low-flow disturbance in perennial rivers have mostly been described in relation to drought events of varying severity and duration that involved progressive flow reduction, or to gradients of intermittency. In four perennial to temporary U.S.A. streams, for instance, 13 taxa (e.g. species of Baetidae, Glossosomatidae, Teloganodidae, Hydropsychidae) decreased in abundance or were eliminated from riffles subjected to a flow disturbance gradient from permanent flow, to dry less than three months, and then more than three months, as compared with nearby permanent sites (Delucchi 1988). Oligochaeta and tipulids, in contrast, were favoured by increasing flow disturbance. Distinct compositional differences among sites also reflected varying associations of families and species with reaches of differing flow permanence in the Winterbourne Stream, U.K. (Wright *et al.* 1984). Hydrological conditions were also a major determinant of assemblage composition over three consecutive midsummer periods in the naturally aseasonal Kowie River, South Africa, with invertebrates responding to a gradient of flow permanency and greatest similarities apparent between assemblages collected under similar flow phases (Uys and O'Keeffe 1997a).

The effects of natural dry-season flows representing the second-lowest discharges on record on invertebrate communities of runs were more apparent in the nutrient-enriched Waipara River than in the near-natural Okuku River, New Zealand, even though the flows were more pronounced in the latter river (Suren *et al*. 2003). Over the six-weeks of summer low flows in the Okuku R., there was no significant change in average number of taxa and invertebrate densities were stable; only a community index of water quality decreased. In the Waipara R., the average number of taxa was also unaltered, but overall invertebrate density increased significantly and abundances of 11 of 18 common taxa were negatively correlated with time since the onset of extreme flows. Additionally, significant decreases in species diversity, evenness and community index scores occurred. These shifts in composition were connected with a switch in dominance from diatoms and cyanobacteria to filamentous green algae with declining flows (Chapter 5). In an unregulated upland Welsh stream, Afon Dulas, an initial reduction in invertebrate abundance occurred during a summer low flow of

40% of normal discharge minima (and at least double their duration), in large part due to reduction in wetted habitat (Cowx *et al.* 1984). Benthic community structure was also detectably altered in the following year. The disturbance effects of a ten week drought were more severe in another small, largely unaltered mountain stream in Wales, Afon Hirnant, which rarely experienced intermittency (Hynes 1958). The majority of insect nymphs and larvae died, and only a few taxa, including *Helmis maugei* larvae, survived prolonged drying in an active form. Dramatic changes occurred in the invertebrate composition in the small, largely perennial (i.e. flow cessation only in very dry years) Waterston Stream, U.K., due to a single summer drought that shifted the flow regime to intermittent and led to reach drying for several months (Ladle and Bass 1981). The majority of invertebrate taxa showed some reduction in numbers or delays in peak abundances (e.g. chironomids, including *Paramerina* sp., oligochaetes), and certain taxa were greatly reduced or even absent. While most taxa re-established post-drought, *Agapetus fuscipes*, a long-lived trichopteran with the dry season its main growth period, as well as a triclad, failed to recover. Other taxa were favoured by the altered flow conditions, or reductions in competition and predation pressures, and showed increased densities (e.g. *Simulium ornatum* and other dipterans, *Ephemerella ignita*). Several taxa appeared unaffected, including ceratopogonids, a trichopteran, and Nematoda.

Responses of invertebrates to severe summer drought (after flow augmentation) were variable and dependent partly on the flow regime characteristics of three reaches of the River Lambourn, U.K. (Wright and Berrie 1987). Flow reduction had a strong disturbance effect on the fauna and habitats of the upper perennial reach, which though still evident further downstream was less severe. Although the number of invertebrate taxa remained similar to that for natural low flows, Shannon-Weiner diversity decreased. While the density of the total invertebrate community increased, reductions in the densities of some Baetidae and Simuliidae occurred with the altered local conditions (e.g. decreased physical habitat and velocities, increased silt levels) accompanying severe flow reduction. In contrast, chironomid larvae were able to effectively exploit the increased food resources and showed increased densities across a range of habitat types. Different responses in individual taxon densities were also reported in a drought-disturbed, perennial English stream (Ledger and Hildrew 2001). The absolute density of nemourids post-drought was often lower than for the equivalent pre-drought period and *Simulium* sp., common before the flow disturbance, was absent thereafter. Conversely, a predatory net-spinning polycentropodid was more abundant in the assemblage following recovery than prior to the drought.

Within the Shillingthorpe section of the River Glen, England, entire drying of the river bed for three summer months due to drought resulted in rapid bioassessment invertebrate scores dropping to zero (Petts *et al.* 1995). Drought that resulted in two months of low flows and negligible flow for a further two months, affecting invertebrates at a time of naturally rapid growth, in perennial Trout Creek, U.S.A., markedly altered benthic invertebrate assemblages, with an overall 50% decrease in total density compared with densities in the subsequent natural-flow year (Canton *et al*. 1984). Habitat loss was identified as the primary cause of the observed low flow effects, in addition to a decrease in suspended food and increased predation. The approx.

80% streamflow reduction precipitated declines in abundances for the majority of taxa, particularly baetids and glossosomatids, while dipterans appeared slightly favoured. Only a few taxa were unaffected by extremely low flows (e.g. *Tricorythodes minutus*, chloroperlid stoneflies). A shift in functional feeding groups occurred with an increase in the relative abundances of shredders and predators, at the expense of normally abundant mayfly-dominated collector-gatherers and collector-filterers (e.g. *Hydropsyche* sp., *Simulium arcticum*). Some 35% of riffle invertebrate taxa investigated showed significant reductions in biomass between the preceding year and a year with extended summer-autumn drought in perennial Glover Creek, U.S.A., attributed to corresponding reductions in hydraulically suitable habitat (Orth and Maughan 1983).

Although most invertebrate taxa survived an unnatural two-week period of flow cessation in a small Danish stream, Milling Baek, with limited declines in abundances, the *Baetis rhodani* population was nearly eliminated (Iversen *et al.* 1978); the authors suggested the last response might be due to a lack of tolerance of the mayfly for zero-velocity habitat, as stream width halved and waters became stagnant. In contrast, invertebrate species abundances were markedly reduced with total streambed drying for several months due to summer drought in another small, slightly altered Danish stream, Orned Baek, previously not subjected to drying for at least five years. With reach desiccation, a common species, *Gammarus pulex*, intolerant of extended drought, along with *Hydropsyche angustipennis* (a species showing only a slight decline in Milling Baek) and *Goera pilosa,* disappeared. Numbers of *Elmis aenea*, however, remained unaltered by the event (also noted by Hynes 1958, but cf. Extence 1981), and oligochaetes and a burrowing mollusc also survived. In contrast, four months of total dryness in a similar, but naturally intermittent stream, Ravnstrup Skovgrøft, in the same catchment, did not detectably alter the presumed pre-adapted community.

The marked decline in summer flows, pool formation and partial riverbed desiccation during a complete drought year in the River Roding, U.K., generally resulted in increased species densities at the most natural site (including orthoclads, *Hydropsyche angustipennis, Athripsodes aterrimus*) due to altered habitat and resource availability, leading to significant changes in community composition (Extence 1981). A few taxa (e.g. *Ancylus fluviatilis*, *Elmis aenea*) were, however, reduced in abundance or even eliminated (attributed in large part to declining water quality; Chapter 5). Species richness remained comparatively high in the perennial Luvuvhu River, South Africa, despite protracted drought that reduced rheophilous taxa, largely as a result of greater numbers of taxa able to cope with standing waters (O'Keeffe and Uys 1998). In contrast, a reduction in the number of taxa by 50% and an almost order of magnitude decrease in total invertebrate density resulted from a halving of the lowest dry-season discharge on record (O'Keeffe and Uys 1998) due to drought over two years in the South African Sabie-Sand River system (Pollard *et al.* 1996; Weeks *et al.* 1996). Changes in assemblage composition were pronounced in riffles, which were highly sensitive to flow reduction, and the isolated refuge pools formed as riffles desiccated, many of which then also dried up over time. Flow-dependent species declined in numbers or disappeared, concomitant with increases in taxa preferring lentic conditions.

Invertebrate populations from riffles and pools were effectively eliminated with exposure to discontinuous flow for over two years, due to an extended drought in the anthropogenically modified, seasonally intermittent, Smiths Branch, U.S.A., even though they had been regularly exposed to low flow stress in the past when the stream naturally briefly ceased to flow late dry season (Larimore *et al*. 1959). Total numbers of invertebrate taxa and relative abundance of individuals were lowest during the dry season in a year of extreme drought, at the start of a seven-year study of the effects on invertebrates of inter-annual flow variability in a third-order coastal stream, Big Sulphur Creek, U.S.A. (McElravy *et al.* 1989). Mean Simpson's diversity and the mean percentage of Chironomidae were also lowest during that year, while a few tolerant taxa, such as the caddisfly, *Gumaga nigricula*, proliferated. While there was a general lack of correlation between the structure of the late dry season invertebrate community and discharge effects across biotopes and years, drought-year riffle assemblages differed distinctly from the rest. By the end of four years of flows lower than any experienced in the previous 20 y (exacerbated by groundwater abstraction), invertebrate abundances and species richness were substantially depressed in the upper, but not lower, reaches of the perennial, Little Stour River, England, with desiccated and sedimented sections most affected (Wood and Petts 1994, 1999); relationships between indices describing the flow disturbance regime and invertebrate response were addressed (Wood *et al.* 2000; Chapter 8). Though few taxa were eliminated, the majority showed reduced densities, including Elmidae, Hydropsychidae, Baetidae, Glossosomatidae, Leptoceridae, Sericostomatidae, Simuliidae, and some other Diptera. In contrast, with the resumption of normal flow, a few taxa disappeared from the impacted reaches (e.g. haliplids) or decreased in abundance, notably taxa favouring slow-flowing habitats (Notonectidae, Corixidae, various Coleoptera). Prolonged low flows were also considered the likely cause of lower than expected macroinvertebrate richness at 80% of the 51 reference sites of the Upper Murrumbidgee River, Australia, with several families absent and increased dominance by Chironominae, Oligochaeta and Simuliidae (Davies *et al*. 2000).

Although extreme dry-season low flows, as a result of a severe one-year drought, at 12 New Zealand river sites in one geographic region generally led to decreases in invertebrate assemblage diversity and the number of sensitive taxa, changes in assemblage composition were not significant when compared with normal conditions (Caruso 2002). Abnormally low flows resulting in partial bed exposure, due to a year of drought in the LaTrobe River, Australia, also had little impact on invertebrate faunal composition, with only an insignificant decrease in richness downstream of some lower sites (Chessman and Robinson 1987). A notable exception was the leptocerid, *Triplectides similis*, which was believed locally absent due to a secondary effect of decreased oxygen (Section 5.1). Invertebrate shredder densities in two headwater streams in the southern Appalachian Mountains, U.S.A., did not differ between two years, despite a drought in the second year that was greater than any experienced in more than 50 years (Cuffney and Wallace 1989).

Different forms of flow regulation that have included discharge reduction (in addition to those described above in relation to stranding and drift) have also variously altered invertebrate composition. Despite

possessing similar mesohabitat diversity the assemblage composition of three English streams was differently affected by flow alteration, quantified based on the percentage deviation of flows under recent hydrological conditions from the historical flow series (Wood *et al*. 1999). Reduced taxon numbers in the rivers Little Stour (flow deficit of -30.8%, reflecting drought plus groundwater overabstraction) and Gadder (-24.1% with water abstraction) were considered to reflect their comparative low-flow stress histories, as compared with higher richness in Mill Stream, which showed a minor flow surplus. Mean invertebrate densities, in contrast, bore no relationship with flow reduction. Of seven South African rivers of varying flow regime permanence, lowest taxonomic richness was found for the Letaba, a naturally perennial river subjected to one tenth of its natural, dry season flow as a result of long-term abstraction (O'Keeffe and Uys 1998). Reduced densities and diversities of invertebrate communities observed in a middle reach of the large regulated Durance River, France, were as a result of the absence of previously available diverse habitats with a reduction in flow to 1/70th of average annual discharge (Cazaubon and Giudicelli 1999). Alteration of flow regimes for water supply at multiple diversion weir and dam sites on the Hawkesbury-Nepean River, Australia, resulted in significantly lower numbers of macroinvertebrate taxa in both riffles and pools at regulated sites than at natural flows (Growns and Growns 2001). The response was attributed to decreases in wetted habitat and the accompanying shift from lotic to lentic conditions with pool formation, rather than altered water quality.

In contrast, with flow regulation in the Brisbane River, Australia, that encompassed discharge reductions and increases from pre-regulation state in different months, there were few marked changes in diversity, total or individual taxon abundances, or mean family richness between regulated and unregulated sites (Choy *et al.* 2000). Changes in the composition of functional feeding groups and in pool biotas, however, were apparent. Total abundance and family richness did not vary significantly spatially above and below a flow regulation structure in Mill Stream, U.K., though they did with season, with the former metric highest at low discharges in the unregulated section (Armitage and Pardo 1995). There also appeared to be no direct effect of 86% to near-total flow abstraction on overall invertebrate density or species richness for a group of flow regulated sites on North Swedish rivers (Englund and Malmqvist 1996).

7.1.4 Use of flow refugia at low flows

Flow refugia enable invertebrates to resist the effects of low-flow perturbation and influence their capacity to recover thereafter (Lancaster and Belyea 1997; strategies of flow refugium use are discussed in Section 1.4.3). The structural and hydraulic heterogeneity of the riverbed offer a diverse range of such sources of protection at different flows, in space and time (Williams and Hynes 1977; Armitage *et al*. 1995; Lancaster and Belyea 1997; Lake 2000), although the relative long-term survival of fauna in different refugia has yet to be established (Lake 2003). In addition to the use of habitat patches of different hydraulic characteristics as low-flow refugia, such as runs or pools, a diverse array of other refugia common to perennial and temporary rivers may be used by invertebrates to secure persistence. Microhabitats that retain water, or are without free water but humid, become essential for the persistence of most invertebrates once low flows become so

severely reduced that exposure and bed drying occur (Humphries and Baldwin 2003; Boulton 2003). Numerous invertebrate species have been reported to utilise moist sediments, damp algal mats, or macrophytes exposed along stream margins or in-channel as temporary refuges at extremely low flows (Moon 1956; Hynes 1958; Larimore *et al*. 1959; Pearson and Franklin 1968; Iversen *et al*. 1978; Ladle and Bass 1981; Wright *et al.* 1984; Canton *et al*. 1984; Boulton 1989; Morrison 1990; Armitage and Petts 1992; Dudgeon 1992b; Boulton and Lake 1992b; Boulton *et al.* 1992b; Stanley *et al.* 1994; Boulton and Stanley 1995; Clinton *et al*. 1996; Pollard *et al.* 1996; Caruso 2002; Boulton 2003).

With regulation by a dam on a British river, a no-flow period of two days after fast flows was tolerated by the downstream benthic invertebrate community, which survived in substratum interstices and within patches of epilithic moss (Armitage and Petts 1992). The reappearance of Oligochaetes soon after drought in four small streams in central Scotland was believed to be due to their survival as adults in damp bed sediments (Morrison 1990). The aquatic leech, *Erpobdella octoculata*, is also a naturally desiccation-resistant taxon commonly known from damp river sediments in perennial U.K. streams (Ladle and Bass 1981). After a ten-week drought in a Welsh mountain stream, numerous members of the original invertebrate assemblage reappeared, several presumed to have survived in moist sediments (among others, stonefly and chironomid species, *Simulium*, *Heptagenia lateralis*; Hynes 1958). With extreme flow reduction in the Sabie River, South Africa, limited numbers of mayflies and caddisflies remained in remnant riffle areas, mainly under wet stones (Pollard *et al.* 1996). Some taxa survived in damp refuges under stones (e.g. Gerridae, *Corydalus cornutus*) or in dry sediments (e.g. a dormant adult water scorpion) with prolonged streambed drying in the largely perennial Smiths Branch, U.S.A. (Larimore *et al*. 1959). Elmids were found in moist substrata of exposed drying riffles, as were Dytiscidae and Hydrophilidae, but were unable to endure prolonged drying. No living individuals of *Gumaga nigricula* survived in dry sediments with two consecutive drought years, in a naturally perennial spring-fed stream (cf. other evidence that Sericostomatidae have used deeper substratum layers as a drought refuge; Resh 1982). Ledger and Hildrew (2001) found no aquatic larvae in riffle substrata that had dried out in a perennial English stream, with the ability of aquatic invertebrates to survive in dry streambed patches appearing limited. Even in intermittent systems, invertebrates may not be able to persist long after total loss of surface water, although exceptions exist (e.g. Boulton 1989; Stanley *et al.* 1994). Few invertebrates survived for longer than five days after total water loss in the U.S. Sycamore Creek (Boulton and Stanley 1995), and only five individuals survived in a desiccated stream reach without damp microhabitats as refugia, for two weeks (Stanley *et al.* 1994). Mats of dried filamentous algae and leaf litter, and sediments below stones, supported a diverse array of invertebrate larvae and adults following drying in intermittent Australian and U.S. desert rivers (Boulton 1989; Boulton and Lake 1992b; Boulton *et al.* 1992b).

The hyporheic zone is widely considered a patchy macroscale refuge from flow disturbance for invertebrates (Williams 1984; Scarsbrook and Townsend 1993; Lancaster and Hildrew 1993a; Hildrew and Giller 1994; Clinton *et al.* 1996). It cannot be assumed to play such a role in all rivers, however (Wallace 1990; Dole-

Olivier *et al.* 1997), with the zone's physical characteristics, event magnitude, and the biota's burrowing capabilities probable factors determining its actual use as a refuge (Palmer *et al*. 1992). Several studies have established the hyporheic zone as an invertebrate refuge from the effects of high flows (Williams 1984; Marchant 1988; Townsend 1989; Yount and Niemi 1990; Brooks and Boulton 1991; Palmer *et al*. 1992; Boulton and Lake 1992b; Townsend *et al*. 1997b; Dole-Olivier *et al.* 1997). In one of few experimental tests of its refuge role, however, Palmer *et al*. (1992) observed only small-scale behavioural migrations of certain taxa downwards into the hyporheic zone during floods.

That the hyporheic zone potentially buffers invertebrate taxa from low-flow perturbations, by providing a refuge from stress and desiccation, as well as a source of recolonisers, has been widely speculated or assumed (Ward 1976; Canton *et al*. 1984; Wright *et al.* 1984; Boulton and Suter 1986; Saltveit *et al*. 1987; Poff and Ward 1990; Boulton and Lake 1992b; Feminella 1996; Pollard *et al.* 1996; Ledger and Hildrew 2001). The literature suggests that its low-flow refuge potential is variable and case specific (Lake 2003), with most use demonstrated for intermittent streams (Williams and Hynes 1977; Boulton 1989). Stehr and Branson (1938) reported various taxa surviving by burrowing deeper into the still-moist bed sediments in a small, naturally intermittent stream, Rock Riffle, U.S.A., with the transition from flowing water to a near-dry bed. Variations in surface discharge were correlated with immediate changes in the invertebrate composition of the shallow hyporheic biotope in Sycamore Creek and other U.S. Sonoran Desert streams (Boulton *et al*. 1992b, c; Boulton and Stanley 1995). Documented cases for the hyporheic zone being a low-flow refuge in perennial rivers are scarce (Dewson *et al.* 2007c), but there are examples pointing towards its use. It was an important short-term refuge for invertebrates stranded with experimental discharge manipulations in the Flathead and Kootenai rivers, U.S.A., with insects moving deeper into the substratum after surface rocks dried (Perry and Perry 1986). Increased abundances in the univoltine stonefly, *Nemoura cinerea,* following total streambed drying of Orned Baek, Denmark, were attributed to nymph survival in the underlying substratum (and reduced competition; Iversen *et al.* 1978). Rapid invertebrate recovery following drought-induced desiccation in perennial Lone Oak Stream, England, was attributed to the influx of larvae from instream refugia, including hyporheic substrata, moist superficial substrata, and small upstream pools (Ledger and Hildrew 2001). Some individuals persisted within the hyporheic zone during an extended period of severe low flows in the perennial groundwater-fed Little Stour R., England (Wood and Petts 1994). With exposure to discontinuous flow for over two drought years in Smiths Branch, U.S.A., Trichoptera, Ephemeroptera, Coleoptera, Diptera, isopods and snails actively resisted extreme flow reduction or conditions associated with desiccation by migrating downward into deeper substratum layers (Larimore *et al*. 1959). Immature chloroperlid nymphs persisted within the hyporheic zone over periods of drying, across a gradient of riffle permanence in four U.S.A. streams (Delucchi 1988). Delucchi (1989) conversely found little vertical movement of invertebrates into the substratum of a permanent stream as riffles became susceptible to drying, in contrast to two temporary streams where it was common.

7.1.5 Influence of low flows on biotic interactions

McAuliffe (1983, 1984) emphasised the potential role of flow disturbance in intensifying or disrupting the dynamics of biotic interactions, notably predation and inter- or intra-specific competition in streams, forcing spatial engagement of species in a series of 'interaction crunches' (Hildrew and Giller 1994). Although the intensity of biotic interactions appears reduced during and immediately following floods (Peckarsky 1983), the converse is believed true for low flow events. It has been considered a flawed assumption that changes in invertebrate composition with low flow phase are entirely attributable to altered abiotic conditions (Boulton and Lake 1992a). Contraction in wetted habitat area and volume, as well as altered hydraulics and resource availability, during low flow periods has been shown to increase the importance of biotic interactions, as well as alter their strength and direction (McAuliffe 1983, 1984; Poff and Ward 1989; Fisher and Grimm 1991; Lake 2000, 2003). For benthic invertebrates, such interactions are most likely to be amplified when individuals are concentrated into smaller, hydraulically less suitable patches or within increasingly isolated pools, leading to increased densities, competition for space or food (e.g. Larimore *et al*. 1959; Extence 1981; Taylor 1983; Boulton and Suter 1986; Lancaster *et al*. 1990; Boulton and Lake 1992a, b; Dudgeon 1993; Pollard *et al*. 1996), and greater likelihood of stochastic community change (Fisher and Grimm 1991). Conversely, biotic interactions may be affected with reductions in densities due to low flow impacts (Feminella and Resh 1990).

In Hong Kong streams, with large-scale natural flow reduction or cessation during the driest months of the year predator impacts were more intense, as predators and prey were brought into closer contact in remaining wetted areas (Dudgeon 1993). With a severe drought following normal flows in Sandy Creek, U.S.A, crayfish were concentrated in isolated pools, leading to increased predation on larger adults (Taylor 1983). Potential differences in predation pressures across hydraulically varied habitat patches might also occur, with shifts in predator and prey distributions in response to flow dynamics, due to taxon differences in hydraulic preferences and the use of specific flow refugia (Lancaster and Hildrew 1993a). For instance, flow mediated interactions between predatory triclad flatworms and their prey, larval blackflies, affected encounter rates (as the taxa had different velocity preferences), prey-handling ability, and provided refugia for prey in higher velocity patches (Hansen *et al*. 1991). Extreme low flows in the River Roding, U.K., shifted predator-prey dynamics, with a previously rare predatory leech, *Helobdella stagnalis*, significantly increasing in numbers in response to increased densities of its main prey, *Asellus aquaticus*, itself responding to increased food availability (Extence 1981). Predation levels were also abnormally elevated in isolated pools under extreme low flows in Smiths Branch, U.S.A. (Larimore *et al*. 1959).

Though competition for dwindling resources is likely to intensify during extreme low flows, this has seldom been documented (Lake 2003). However, a decline in Chironominae numbers during extremely low flows in the River Roding, concurrent with a large-scale increase in Orthocladiinae, a group seeming tolerant of or favoured by drought conditions, was proposed to be the result of competition (Extence 1981). Further, several studies have addressed the topic at natural low flows. For example, intraspecific competition was

shown to be pervasive for a *Helicopsyche borealis* population in Big Sulphur Creek, U.S.A., at summer low flows, due to high larval densities and competition for periphyton food (Lamberti *et al.* 1987, cited in Feminella and Resh 1990); high-flow disturbance also influenced intraspecific competition intensity in the same species (Feminella and Resh 1990). McAuliffe (1984) experimentally demonstrated that natural, seasonal flow reduction in Owl Creek, U.S.A., interrupted the formation of monopolies by *Leucotrichia pictipes*, a sessile trichopteran that shared overlapping microhabitats with several other species for which distributions and abundances were limited through inter-specific competition.

7.1.6 Recovery from low-flow disturbance

Many studies of invertebrate recovery post-disturbance have focused on flood or simulated physical disturbances, where recovery is often rapid and from a variety of sources (e.g. Gray and Fisher 1981; Fisher *et al*. 1982; Scrimgeour *et al*. 1988; Lake *et al.* 1989; Boulton and Lake 1992b; Dudgeon 1993; Miller and Golladay 1996; Matthaei *et al*. 1997). Effects of low-flow disturbances may also be short-lived with invertebrates typically showing rapid recovery, using similarly diverse routes for perennial and intermittent rivers (Larimore *et al.* 1959; Harrison 1966; Townsend and Hildrew 1976; Iversen *et al.* 1978; Extence 1981; Canton *et al*. 1984; Delucchi 1988; Frid and Townsend 1989; Townsend 1989; Morrison 1990; Quinn and Hickey 1990; Yount and Niemi 1990; Dudgeon 1992b; Caruso 2000; Boulton 2003; Section 1.4.3 provides further discussion). For example, recovery was initiated three days after re-wetting and complete by at most 38 days in perennial Lone Oak Stream, southern England, following a drought that led to desiccation of the majority of the streambed for about two months (Ledger and Hildrew 2001). Such rapid recovery may be in large part due to the long disturbance history of natural drought experienced by most aquatic ecosystems (Boulton 2003), including the natural predictable low-flow disturbance cycles to which intermittent systems are particularly attuned (Boulton and Lake 1992b; Pires *et al*. 2000). Unpredictable, extreme low flows in naturally perennial rivers can, however, have marked and long-lasting impacts on invertebrate populations (Niemi *et al.* 1990; Boulton and Lake 1992b; Boulton *et al.* 1992a; Lake 2000). Biotic response to more predictable events, such as seasonal droughts, tends to be characterized by high resistance and strong resilience (Lake 2003; e.g. Boulton and Lake 1992a; Stanley *et al.* 1994; Uys and O'Keeffe 1997a; Pires *et al.* 2000; Boulton 2003). In comparison, invertebrate response to less predictable perturbation events typically involves low to moderate resistance levels and variable resiliency (e.g. Ladle and Bass 1981; Boulton and Lake 1992a, b; Wood and Petts 1994, 1999; Caruso 2002; Boulton 2003). The degree of resistance or resilience to low-flow disturbance appears at least group- if not also species-specific (Lake 2003). For instance, different recovery rates were reported across various pool types and taxa, after resumption of normal flows following protracted severe low flows in the Sabie River (Pollard *et al.* 1996). Certain ephemeropterans were able to recover rapidly as wetted habitat became available, while trichopterans showed limited recolonisation.

Patterns of recovery differ according to the type of low-flow perturbation (Lake 2003), and its timing, intensity and duration (Larimore *et al*. 1959; Boulton 2003). Abundances generally appear to attain pre-

disturbance levels more rapidly than species richness (e.g. Iversen *et al*. 1978; Cowx *et al*. 1984). Faunal recovery from seasonal droughts tends to be rapid, with predictable sequences of taxa (Lake 2003), and recolonisation from refugia important in the process (e.g. Harrison 1966; Boulton and Lake 1992b; Miller and Golladay 1996; Pires *et al*. 2000). Recovery from less predictable low-flow disturbances appears more variable on a case-specific basis, and may involve populations of transient taxa and depletion of characteristic lotic fauna (Lake 2003). Recovery may still be relatively rapid, at typically within one year (Niemi *et al.* 1990; e.g. Larimore *et al.* 1959; Townsend and Hildrew 1976; Ladle and Bass 1981; Canton *et al.* 1984; Morrison 1990; Weeks *et al.* 1996; Ledger and Hildrew 2001; Caruso 2002). Although the Welsh stream, Afon Dulas, was entirely flow disturbed due to drought, recovery occurred within two years (Cowx *et al.* 1984). With a return to normal flows following four drought years in the perennial Little Stour River, England, full recovery took about three years, with identification of the absolute endpoint difficult, while an approximately one-year drought in the same stream had a less protracted impact (Wood and Petts 1994, 1999).

In some instances, certain species are eliminated with severely reduced flows and appear unable to recover (e.g. Hynes 1958; Iversen *et al.* 1978; Ladle and Bass 1981; Weeks *et al.* 1996). For instance, a common amphipod and chironomids, *Polypedilum* sp. and *Macropelopia* sp., were effectively eliminated from a largely perennial U.K. stream, due to a single summer drought (Ladle and Bass 1981). Losses in abundant species have caused major changes in community structure and lags in recovery, for example where taxa persisted during the early stages of a low-flow perturbation but showed unsuccessful recruitment the following year, even with a return to more normal flows (e.g. Resh 1982; Boulton and Lake 1992b; Boulton 2003). There may also be gains in new taxa with the recovery process (e.g. Harrison 1966; Ladle and Bass 1981; Boulton and Lake 1992b). Transient dipteran species appeared within a few days after natural flow resumed in a seasonal southern African stream, proliferating rapidly before being replaced by characteristic permanent stream species (Harrison 1966).

The ability of invertebrates to recover from low flow-disturbance is dependent on factors including: season and flow conditions; availability of and access to refuges, which effectively links physical habitat complexity, fragmentation extent, proximity to permanent water, and taxon life history attributes; the extent of the affected area and degree of alteration (including by type of habitat); and the ability for general habitat recovery (Larimore *et al*. 1959; Williams and Hynes 1976; Gray and Fisher 1981; Cowx *et al.* 1984; Stanley and Fisher 1992; Boulton and Stanley 1995; Lake 2000; Boulton 2003). All major avenues of invertebrate redistribution or recolonisation have been shown to be important in recovery (as outlined in Section 1.4.3).

7.2 APPROACH AND OBJECTIVES

Within this chapter, an attempt was made to identify any direct responses shown by benthic macroinvertebrate assemblages, from those outlined above, to potential disturbance effects of altered patterns

of low flows; invertebrate drift was not explicitly addressed. Effects of both natural and experimentally manipulated low flows were sought at several spatial scales: (1) across multiple rivers; (2) the individual site (river reach) and locations within it; (3) the hydraulic biotope mosaic, for riffles, runs and pools (defined in Chapter 6); and (4) stone microhabitats. Data disaggregation to finer spatial or temporal resolution was used to both improve detection of effects and confirm patterns suggested at coarser scales. Thesis hypotheses and main objective 4 (Section 1.2 and Figure 1.2) were addressed by focusing on the following secondary objectives to:

1. Determine the direct effects of natural and unnatural low flow regimes on the overall composition of benthic macroinvertebrate assemblages.
2. Explore the extent of association of invertebrate assemblages with hydraulic biotopes, as well as any changes in such associations at natural and extreme low flows.
3. Examine any shifts in invertebrate microdistribution patterns that might represent responses to flow-mediate changes in local conditions.
4. Identify general patterns of diversity of invertebrate assemblages among biotopes at low flows.
5. Investigate direct species-level responses to low-flow disturbance using the Chironomidae as a focal group.

Field, laboratory and analytical methods are detailed in Section 3.5. The main results, presented in Sections 7.3 to 7.7, were directed at assessing responses of entire assemblages (at family taxonomic level) to natural and unnatural low flows. Recovery from low-flow disturbance was not a main focus of the study, though briefly addressed in relation to the reinstatement of natural discharges post-impact. In Section 7.3, spatiotemporal changes in overall invertebrate assemblage composition in response to low flow regime were identified for the rivers. Section 7.4 addresses finer-scale assemblage-biotope patch associations at low flows, in preparation for investigations of biotope and hydraulic specificities of individual taxa in Chapter 8. Invertebrate microdistribution patterns at low flows are described in Section 7.5. Section 7.6 deals with general patterns in assemblage diversity relative to low flow regime in different reaches and across biotopes. In Section 7.7 (as also in Chapter 8), Chironomidae were used for select analyses, to ascertain the extent to which species-level responses were consistent with those at family level. In the final section, findings were consolidated and discussed in preparation for the characterization of ecologically-relevant low flows in Chapter 8.

7.3 EFFECTS OF LOW FLOWS ON OVERALL COMPOSITION OF INVERTEBRATE ASSEMBLAGES

7.3.1 Spatial and temporal changes in family-level composition of invertebrate assemblages in relation to low flow regime

Differences in assemblage composition across rivers

A first analysis of differences among benthic macroinvertebrate assemblages pooled from all reaches (as recommended by Niemi *et al.* 1993) over the duration of the low flow study, based on the presence or absence of families or higher taxa (hereafter simply referred to as families; Appendix 7.1) showed no clear grouping of assemblages on the grounds of individual sites (river reaches), locations within each reach, or season (and hence, month or flow regime). Moreover, the ordination stress was unacceptably high (0.27; Section 3.5). Broad-scale catchment affinities were however apparent. In contrast, analysis based on abundances showed a clear first division, just above 60% Bray-Curtis similarity, into two clusters reflecting the catchment affiliations of the sites (Figures 7.1a, b); a similar result was obtained in the pilot study (Chapter 2). Further separation of the Du Toits and Riviersonderend sites occurred at 65% similarity, with the other sites more similar to each other in assemblage composition. Although there was some evidence of seasonal separation of assemblages, particularly with the transition from the dry season to autumn, it was only partial.

Under natural flow conditions, at the control site (Elands) the mix of assemblages reflected high variability in invertebrate composition between reach locations and across months, with no within-season biotic response to low flow regime (Chapter 4). Comparison of assemblages for the flow reduction phase showed no major or obvious separation out of flow-impacted assemblages across sites. Moreover, similarities among all assemblages were fairly high (e.g. when compared with the results for a larger group of rivers; Chapter 2). Within-site effects of reduced discharge were limited and most obvious using classification. Results were only weakly supported by the ordination plot, which was only useful for exhibiting broad trends. At the Molenaars site, the effects of abnormal flow reduction appeared non-existent at this level of analysis, throughout the peak dry season (Figures 7.1a, b). In fact, the most similar assemblages overall were for the March control and impact sub-reaches (87%). The extreme flow-impacted assemblages for both months also were similar. In contrast, for the Du Toits site, the February flow-impacted assemblage differed in composition from the corresponding control assemblage, as well as from all other assemblages sampled, separating at 73% similarity (Figure 7.1a). Although the ordination showed high divergence between control and impact samples, results could not be considered conclusive as similar degrees of divergence were also apparent outside of the months of extreme low flows (Figure 7.1b). In the case of the Riviersonderend reach, although there was little difference in overall assemblage composition initially with flow reduction (February: RC02 cf. RI02), the impacted assemblage diverged markedly from the assemblage experiencing natural low flows in March (Figure 7.1a). The result suggests a delayed yet demonstrable response of the

benthos to extreme low flows in this river, though the difference was less apparent in the ordination plot (Figure 7.1b).

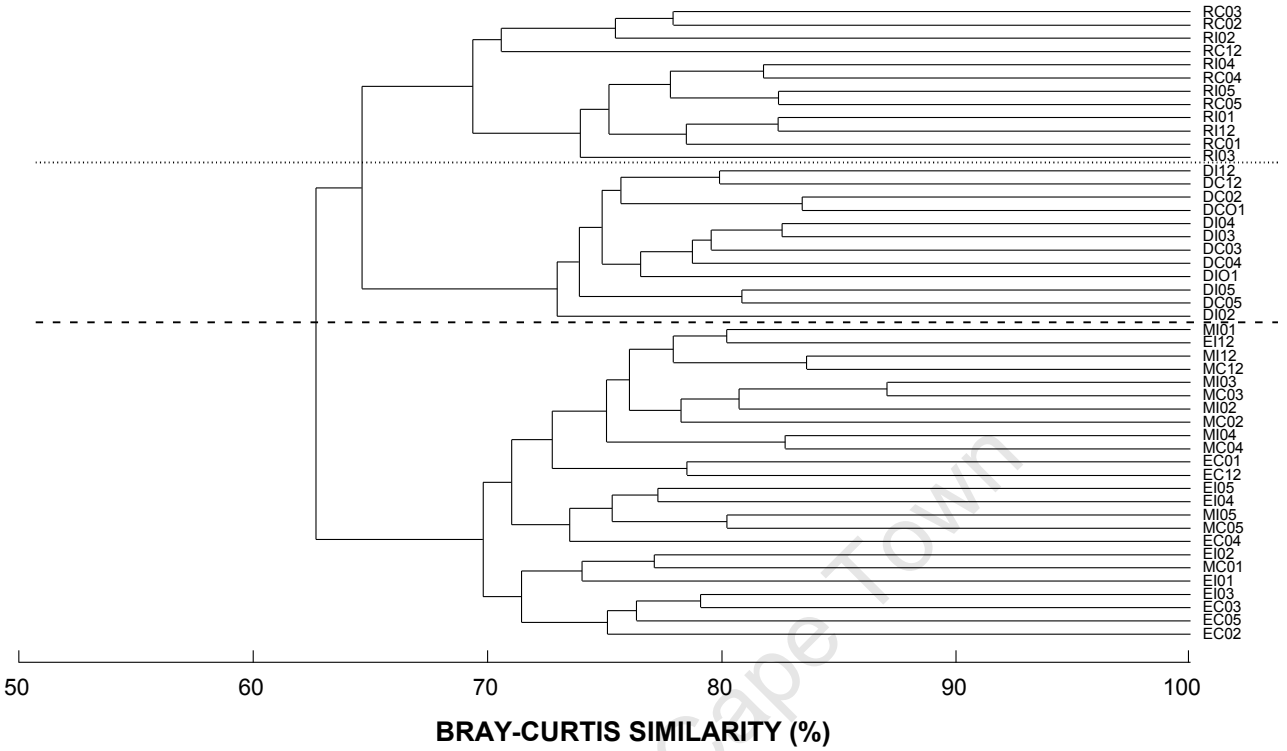


Figure 7.1a Dendrogram of whole-stone invertebrate samples (irrespective of biotope type) based on mean family abundances (0.1 m^{-2}) from site locations over the study duration. E - Elands; M - Molenaars; D - Du Toits; R - Riviersonderend; C - control location; I - impact location; 12-05 indicates month, from Dec-May. Primary (dashed line) and secondary (dotted line) group divisions are indicated. Semi-quantitative data from the substratum underlying stones (i.e. U sample parts) were excluded (Section 3.5).

Analysis of similarities revealed that the large-scale differences in invertebrate assemblages among sites, on average, were highly significant (Global R = 0.808, P = 0.001; Table 7.1), despite any influences attributable to location, month (season), low flow treatment, or biotope type. Pairwise tests further indicated that all sites differed significantly from one another (P = 0.001), but supported the observed relatively high and low overlaps in character between the Elands and Molenaars, and Elands and Du Toits, assemblages, respectively (Table 7.1). Results were mostly in concordance with those of the pilot survey, where all four sites were found to be significantly different, but the Du Toits and Riviersonderend were the most biologically similar river pair (Chapter 2).

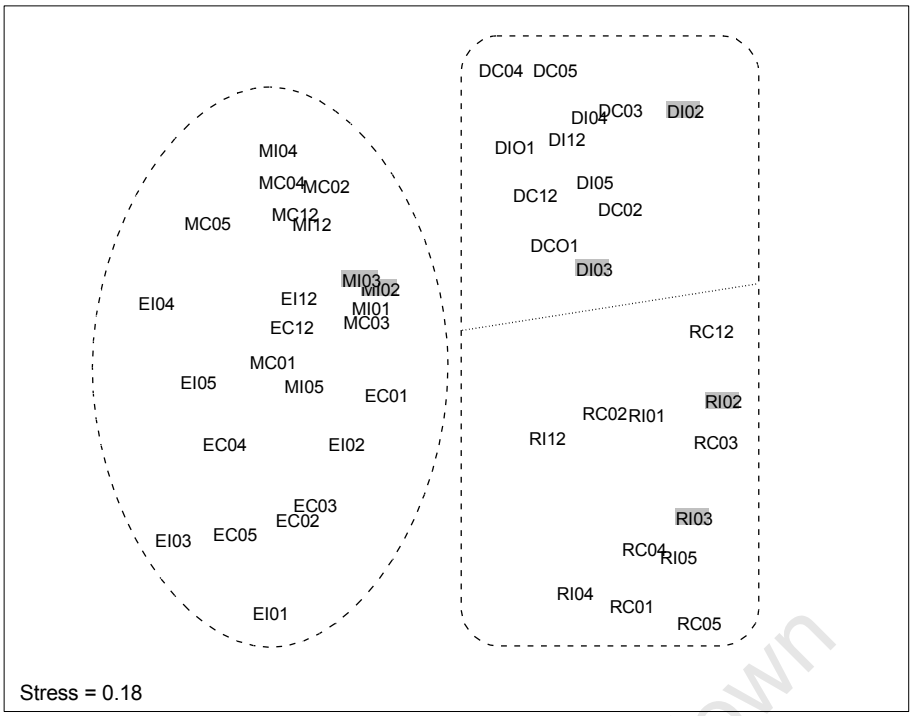


Figure 7.1b Ordination plot based on the same similarity matrix as Figure 7.1a. Primary (dashed line) and secondary (dotted line) dendrogram group divisions are superimposed. Assemblages subjected to extreme low flows during the impact phase are shaded. Abbreviations as per Figure 7.1a.

Table 7.1 One-way ANOSIM results for comparisons of invertebrate assemblages sampled from all sites and locations over the study period. R statistics for site pairwise tests are followed by P values in parentheses. Samples represented mean family-level abundances (0.1 m^{-2}).

FACTOR		PAIRWISE TESTS FOR GROUPS				
Site			Elands	Molenaars	Du Toits	Riviersonderend
Global R	0.808	Elands		0.420 (0.001)	0.957 (0.001)	0.893 (0.001)
P	0.001	Molenaars			0.888 (0.001)	0.940 (0.001)
		Du Toits				0.830 (0.001)
		Riviersonderend				

Based on these findings, a SIMPER analysis was conducted which indicated high within-site similarities in assemblage composition at family level above 70%: highest at 75% (Molenaars) and lowest at 73% (Riviersonderend). Invertebrate families primarily responsible for differences in assemblage composition between site pairs and hence, retention of catchment signatures, are listed in Appendix 7.2. Such differences were most attributable to variations in the relative abundances of certain, typically common families, rather than their presence or absence.

Between the most similar sites (30% dissimilar), the Elands and Molenaars, family abundances were greater for the latter site, except in the case of Teloganodidae and Helodidae. Mean abundances of simuliids (17.6 cf. 88.3 0.1 m^{-2}) and baetids (197.2 cf. 385.4 0.1 m^{-2}) contributed the greatest cumulative percentage contribution to inter-site differences, followed by chironomids. Significant differences in assemblage composition between the Molenaars and Du Toits also were attributed to several families, with greatest individual contributions in percentage dissimilarity due to lower numbers of notonemourids (0.1 cf. 7.0 0.1 m^{-2}), as well as higher hydropsychid and heptageniid densities in the former reach. The Du Toits and Riviersonderend sites were characterised by an average dissimilarity of 35%, with an absence of caenids in the latter reach (cf. 7.4 0.1 m^{-2}), and an elevated simuliid population in the Du Toits (238.0 cf. 7.4 individuals 0.1 m^{-2}). Four families contributed most to the difference in invertebrate composition (on average 38%) between the Elands and Riviersonderend reaches (viz. Heptageniidae, Baetidae, Teloganodidae, Hydropsychidae), all of which were significantly more abundant in the Elands. Apart from numbers of hydroptilid caddis (3.7 cf. 0.7 0.1 m^{-2}), the Riviersonderend recorded lower numbers than the Molenaars of all taxa contributing most to the differences in site assemblage composition (39%). Baetids, heptageniids, simuliids and hydropsychids were primarily responsible for the observed differences overall. As indicated by the ANOSIM results, the lowest similarity was observed for the Elands and Du Toits sites (39% dissimilarity). Several families drove the differences, most notably Simuliidae and Chironomidae, for which densities were elevated in the latter reach.

Families were effectively absent in only three instances, contributing to relative dissimilarity, all for the Riviersonderend site: Limnichidae, Heptageniidae and Caenidae. However, re-examination of site pilot data (Appendix 2.2) for riffle samples that included multiple substratum layers showed that typically only caenids did not occur in the reach. Although uncommon, limnichids were found in the pilot survey, as well as in the underlying substratum for the current study. Heptageniids were also encountered in the pilot survey, albeit at low densities (Chapter 2), though curiously not in the main study.

A one-way ANOSIM addressing the apparent variations in benthic composition between site control and impact locations (Figures 7.1, b) demonstrated that the significant difference obtained (Global R = 0.665, P = 0.001) was entirely site related (Table 7.2). There were no significant differences detected between control and impact locations for individual sites (Table 7.2). Similarly, an assessment of whether or not there were significant differences in assemblage composition among months revealed no gross-scale seasonal differentiation (Global R = 0.018, P = 0.319; Table 7.2), with samples representing early, peak and late summer, as well as early autumn, intermixed (Figures 7.1a, b). Least separation of assemblages was found mid-summer (Feb-Mar: R = -0.127, P = 0.972). As envisaged, the difference in composition between seasonal 'extremes' (as represented by Dec and May), though relatively weak was significant (R = 0.231, P = 0.033). The results confirmed the lack of an appreciable effect of low flow regime at this scale, necessitating closer examination of invertebrate patterns characterizing individual sites.

Table 7.2 One-way ANOSIM results for comparisons of invertebrate assemblages sampled from different locations (control – C vs. impact - I) and months for the sites. R statistics for pairwise tests are followed by P values below, in parentheses. Significant results ($P \leq 0.050$) in italics.

FACTOR			PAIRWISE TESTS FOR GROUPS								
	Global R	***P***		EL C	EL I	MO C	MO I	DU C	DU I	RI C	RI I
Location	*0.665*	*0.001*	EL C		0.054 (0.325)	*0.533 (0.002)*	*0.513 (0.004)*	*0.965 (0.002)*	*0.978 (0.002)*	*0.893 (0.002)*	*0.872 (0.002)*
			EL I			*0.409 (0.004)*	*0.257 (0.030)*	*0.935 (0.002)*	*0.917 (0.002)*	*0.924 (0.002)*	*0.915 (0.002)*
			MO C				-0.122 (0.810)	*0.844 (0.002)*	*0.922 (0.002)*	*0.944 (0.002)*	*0.930 (0.002)*
			MO I					*0.806 (0.002)*	*0.883 (0.002)*	*0.933 (0.002)*	*0.930 (0.002)*
			DU C						-0.120 (0.883)	*0.791 (0.002)*	*0.804 (0.002)*
			DU I							*0.844 (0.002)*	*0.804 (0.002)*
			RI C								-0.156 (0.939)
			RI I								
Month	0.018	0.319		Dec	Jan	Feb	Mar	Apr	May		
			Dec		0.011 (0.352)	-0.038 (0.579)	0.100 (0.142)	0.042 (0.280)	*0.231 (0.033)*		
			Jan			-0.065 (0.758)	-0.031 (0.555)	0.004 (0.387)	0.046 (0.271)		
			Feb				-0.127 (0.972)	-0.057 (0.691)	0.113 (0.129)		
			Mar					-0.062 (0.739)	0.049 (0.233)		
			Apr						-0.003 (0.405)		
			May								

Differences in assemblage composition within individual site reaches

Classification and ordination analyses of individual sites still yielded little information on potential effects of season (month) or location, and hence extreme low flow effect, on family-level invertebrate composition at individual sites. For the Elands River, there was no coherent grouping of assemblages by season (or, as expected given that both locations were subjected to the same natural flows, by location). Moreover, probably as a function of the variability encountered in individual samples, overall similarity in assemblage composition was only 27%; ordination results supported this finding (stress level = 0.19). Apart from a couple of small dendrogram clusters of samples for December and May, the results for the Molenaars site were similar to those of the Elands, with considerable inter-mixing of samples from different months and locations (though with 39% similarity among all samples; stress = 0.20). Similar results were also obtained for the Du Toits site, where classification and ordination results indicated the highest degree of difference among assemblages from different months and locations, with only 20% similarity across all of them, as well as several outliers. Although greatest within-site separation of assemblages into groups was most distinct for

the Riviersonderend reach, with overall assemblage similarity also low at 33%, the resultant ordination stress level was high (0.22).

The lack of assemblage response to flow disturbance at this scale again pointed to a need for closer examination of the data. An attempt was made in the next section to identify assemblage-level responses of invertebrates to low flows at individual sites, specifically for study impact and post-impact phases, following an assessment of patterns in assemblage composition under natural flows in early summer (the pre-impact phase).

7.3.2 Invertebrate assemblage composition during different low-flow phases

Assemblage composition under natural flows in early summer

Analysis of similarities for the two locations at each site typically showed no significant differences in assemblage composition during early summer, as anticipated (Table 7.3). Natural variability was only significantly high for the Du Toits reach in January, and at a low Global R value.

Table 7.3 One-way ANOSIM results for comparisons of invertebrate assemblages from control and impact locations during the pre-impact phase, for individual sites. Significant Global R statistics for the factor, location, are in bold.

SITE	*N* PER FACTOR GROUP	ELANDS		MOLENAARS		DU TOITS		RIVIERSONDEREND	
FACTOR GROUP		Global R	*P*	Global R	*P*	Global R	*P*	Global R	*P*
Overall pre-impact phase	18	0.059	0.069	0.007	0.311	0.050	0.081	0.056	0.059
December	9	0.086	0.138	-0.027	0.554	0.002	0.410	0.021	0.276
January	9	0.061	0.164	-0.005	0.428	**0.148**	**0.038**	0.019	0.325

Changes in assemblage composition linked to natural and extreme low flows mid-summer

A priori-based ANOSIM comparisons of assemblages (all biotopes combined - see Sections 7.4.1 and 7.4.2, for biotope-specific analyses) from control and impact locations at sites, targeting the lowest flow months (impact phase, Feb-Mar) are presented in Table 7.4. Given previous indications of the inherent variability in benthic composition in the Elands reach, it was perhaps not surprising that the control site was the only one exhibiting a significant inter-location difference mid-summer, though only in March. Although the difference was significant, the corresponding low Global R value suggested a negligible effect. A marginally increased inter-location difference in assemblages was apparent in February for the Du Toits reach, and in March for the Riviersonderend reach; the Molenaars site showed little difference.

Table 7.4 One-way ANOSIM results for comparisons of invertebrate assemblages from control and impact locations during the impact phase, for individual sites. Significant Global R statistics for the factor, location, are in bold.

SITE	*N* PER FACTOR GROUP	ELANDS		MOLENAARS		DU TOITS		RIVIERSONDEREND	
FACTOR GROUP		Global R	*P*	Global R	*P*	Global R	*P*	Global R	*P*
Overall impact phase	18	-0.013	0.568	-0.056	0.990	-0.014	0.610	0.052	0.096
February	9	-0.051	0.695	-0.108	0.964	0.064	0.155	0.037	0.243
March	9	**0.153**	**0.047**	-0.098	0.982	-0.047	0.741	0.058	0.185

Recovery of invertebrate assemblages with reinstatement of natural flows

There appeared to be no evidence of delayed or incomplete recovery from any low flow disturbance after natural discharges were reinstated in the flow-impacted reach sections. This was confirmed by an ANOSIM of the two groups comprising invertebrate assemblages from the location pairs at all sites, for the period following extreme low flows, with no significant effects and moreover, little apparent difference between results for early or later stages of the post-impact phase (Table 7.5).

Table 7.5 One-way ANOSIM results for comparisons of invertebrate assemblages from control and impact locations during the post-impact phase, for individual sites.

SITE	*N* PER FACTOR GROUP	ELANDS		MOLENAARS		DU TOITS		RIVIERSONDEREND	
FACTOR GROUP		Global R	*P*	Global R	*P*	Global R	*P*	Global R	*P*
Entire phase	18	0.019	0.242	-0.018	0.682	0.003	0.367	-0.011	0.549
April	9	-0.047	0.721	-0.036	0.662	-0.010	0.420	0.086	0.134
May	9	0.052	0.166	-0.075	0.840	0.067	0.108	0.015	0.326

Based on the results of these various exploratory analyses, any effects of low flows, including extreme flow reduction, were clearly limited and/or masked by other factors at family level, principally site biophysical character and the inherent variability in invertebrate assemblage composition spatially and in time.

7.4 INVERTEBRATE ASSEMBLAGES OF DIFFERENT BIOTOPES AT NATURAL AND EXTREME LOW FLOWS

7.4.1 Composition of invertebrate assemblages of different biotopes, across sites and months

Classification and ordination analysis invertebrate assemblages from different biotopes, across all sites and months, showed only the separate groupings of the Elands and Molenaars assemblages on one hand, and those of the other two sites on the other, reflecting again the dominance of river system signatures (as per

Section 7.3.1); ascription of assemblages to main biotope types was based on the hydraulics-based field classification validated in Chapter 6. There was no differentiation of assemblages on the basis of biotope type, month, or low flow state. Moreover, similar but independent analyses of only riffle, run, or pool assemblages remained consistent in reflecting a far greater influence of individual river character on sample affinities than any other factors; these results affirmed the necessity of the finer scale analyses below.

7.4.2 Spatiotemporal associations of invertebrate assemblages with different biotopes at individual sites

Classification and ordination of invertebrates sampled from the main biotopes at each site were used in combination with ANOSIM and SIMPER, for sample groups designated *a priori*, to assess the association of assemblages with particular biotopes, with reference to reach locations, month and hence, low flow regime. The Elands site did not exhibit any distinct grouping of assemblages in relation to location or month, but showed some clustering by biotope type (Figures 7.2a, b). In particular, there was considerable overlap of pool and run fauna, more so than for the other sites. Riffle benthos tended to cluster separately, with little overlap with that of runs and none with pool assemblages (Figure 7.2a; Table 7.6). Pairs of samples (representing means) from the two site locations, both reflecting natural conditions, in the same month varied considerably in their degree of separation in ordination space - for instance, from low in the case of runs in April, to high for runs in February (Figure 7.2b). This pattern suggested high variability in assemblage composition and/or low group affinities above a base similarity of 52% (Figure 7.2a).

These findings were supported by the results of a two-way crossed ANOSIM of the influence of biotope and location for the Elands site. There was no significant difference between locations at this scale (Global R = -0.026, P = 0.646), as at coarser scales of resolution (see previous sections), but a highly significant difference in the composition of assemblages from different biotopes (R = 0.415, P = 0.001; Table 7.6). Given this result, data for the two Elands locations were pooled (as done for the other sites) for a one-way ANOSIM, generating increased power to detect relative differences in assemblage biotope specificity. The outcome was a significant difference, on the basis of pairwise tests, among the invertebrate assemblages of riffles, runs and pools, for all sites (Table 7.6). As the most hydraulically distinct biotopes (Chapter 6), greatest assemblage differentiation occurred between pools and riffles (R = 0.793, P = 0.001; also the case at the other sites). The weakest, albeit still significant, assemblage differentiation was found for pools and runs (R = 0.217, P = 0.003).

The SIMPER analyses for the Elands data indicated that the internal similarity of all biotopes was based primarily on the relative abundances of only the three numerically dominant families: Baetidae, Simuliidae and Chironomidae (Appendix 7.3a provides detailed information on the relative contributions, based on average abundances, of individual families to dissimilarities between biotope types). Greatest intra-biotope similarity, and hence consistency in composition, was found for riffles (68%), followed closely by pools (66%) and runs (65%).

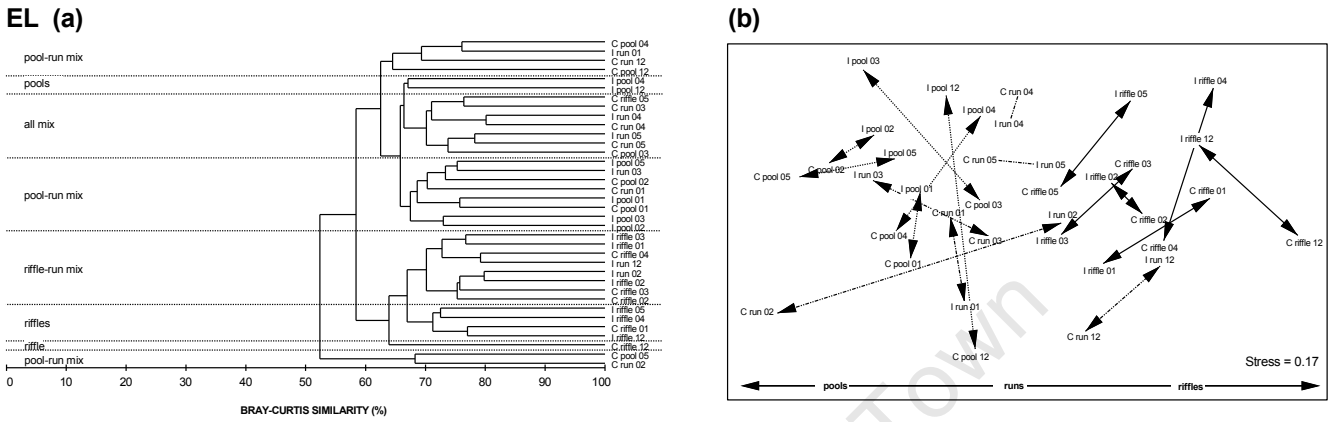


Figure 7.2 **(a) Dendrogram of assemblages from different biotopes (mean family abundances 0.1 m^{-2}) for control (C) and impact (I) locations at the Elands site.** 12-05 indicate month (Dec-May). Principal group divisions are demarcated by dotted lines. **(b) Corresponding ordination plot**. Sample pairs are indicated by lines with two-way arrows: riffles (solid), runs (dot-dash), pools (dot).

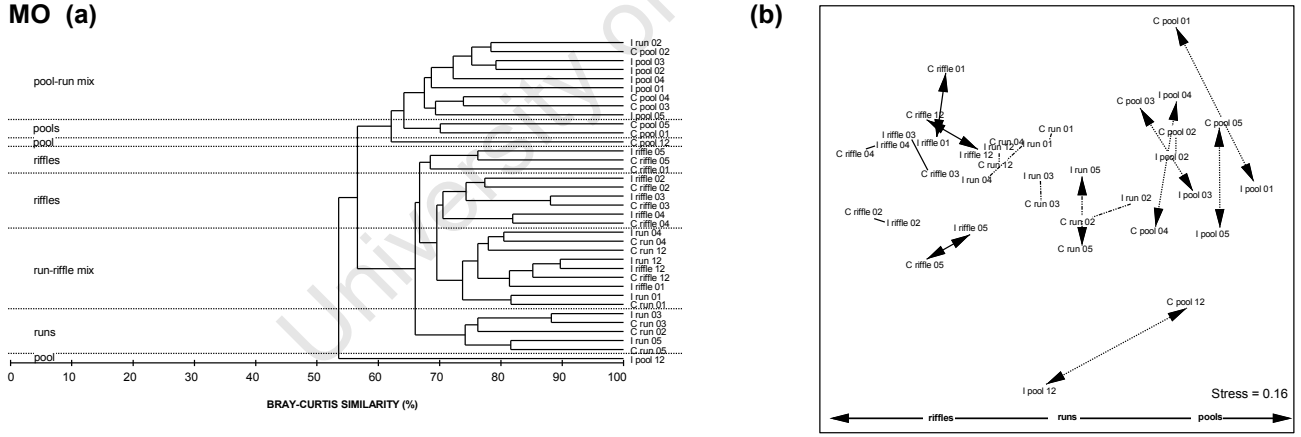


Figure 7.3 **(a) Dendrogram of assemblages from different biotopes (mean family abundances 0.1 m^{-2}) for control (C) and impact (I) locations at the Molenaars site. (b) Corresponding ordination plot**.

Table 7.6 Results for ANOSIMs comparing invertebrate assemblages sampled from different locations and hydraulic biotopes, for each site. Samples represented mean family-level abundances (0.1 m^{-2}) per biotope type. Significant results are shaded.

SITE AND FACTOR(S)	ELANDS		MOLENAARS		DU TOITS		RIVIERSONDEREND	
	R	*P*	R	*P*	R	*P*	R	*P*
Location x Biotope								
Global: Location	-0.026	0.646	-0.022	0.599	-0.086	0.935	-0.026	0.670
Global: Biotope	0.415	0.001	0.634	0.001	0.521	0.001	0.338	0.001
Biotope								
Global	0.447	0.001	0.626	0.001	0.533	0.001	0.339	0.001
Pairwise tests for groups								
riffle vs. run	0.320	0.002	0.541	0.001	0.485	0.001	0.152	0.005
riffle vs. pool	0.793	0.001	0.898	0.001	0.812	0.001	0.589	0.001
run vs. pool	0.217	0.003	0.532	0.001	0.334	0.001	0.273	0.001

Comparison of riffle and run assemblages yielded an average dissimilarity of 39%, with most difference attributable to higher mean abundances of nine families in riffles (Appendix 7.3a). Only leptocerids were found in greater densities in runs than riffles (1.2 cf. 0.5 0.1 m^{-2}). The single greatest contributor to percentage dissimilarity was the Simuliidae, reaching average densities of 49.4 individuals 0.1 m^{-2} in riffles, as compared with 2.7 individuals 0.1 m^{-2} in runs. Baetids, hydropsychids and chironomids were also key contributors to the difference in assemblages. The high ratio of average contribution to group dissimilarity versus standard deviation (1.56) highlighted the Philopotamidae (*Chimarra* spp.) as a potential discriminatory family for these two biotopes (Clarke and Warwick 2001), with higher abundances in riffles than runs. Analysis of riffle and pool assemblages showed the same five main taxa contributing to the observed dissimilarity as for the comparison of the former with runs (Appendix 7.3a). Notably, the greatest contributor to biotope dissimilarity was the Simuliidae, only occasionally present and in low numbers in pools (0.9 0.1 m^{-2}, possibly incoming drift of dead larvae), as compared with the higher densities recorded for riffles and runs above. Hydropsychidae also occurred in very low numbers in pools (0.2 0.1 m^{-2}) as compared with riffles (11.3 0.1 m^{-2}), and the ratio of 3.07 for average contribution to SD identified this family as an indicator of biotope affinity. Riffles were also represented by the presence of hydroptilids, which were absent from pool stones. Pools and runs, though the most similar pair, exhibited differences in baetid and teloganodid abundances in particular, with highest numbers of both families recorded in the former biotope (156.3 versus 125.4 individuals 0.1 m^{-2} and 76.1 versus 40.2 individuals 0.1 m^{-2}, respectively). Leptophlebiidae and leptocerid caddisflies were also most abundant in pools (Appendix 7.3a). In contrast, the majority of taxa contributing to biotope differences were found in higher numbers in runs. The average contribution: SD ratio (1.69) highlighted the Chironomidae as a possible discriminator family between pools and runs (see also Section 7.7).

The lack of seasonal separation of the Elands assemblages (Figures 7.2a, b) also was borne out by the results of a one-way ANOSIM for month with no significant difference in composition, on average, across months (Global R = 0.068, *P* = 0.125; Table 7.7). However, as at all other sites, pairwise tests showed a detectable difference in assemblages between the commencement (Dec) and end of the dry season (early May - shift to autumn conditions), with R = 0.274 (*P* = 0.030). A SIMPER analysis, the full results of which are given in Appendix 7.4, indicated depressed numbers of simuliids and baetids, in particular, in May as compared with early summer.

Table 7.7 Results for ANOSIMs comparing invertebrate assemblages sampled from different months (biotopes pooled), for each site. Samples represented mean family-level abundances (0.1 m^{-2}). Significant results are shaded.

SITE AND FACTOR	ELANDS		MOLENAARS		DU TOITS		RIVIERSONDEREND	
	R	*P*	R	*P*	R	*P*	R	*P*
Month								
Global	0.068	0.125	0.059	0.140	0.105	0.031	0.144	0.008
Pairwise tests for groups								
12 vs. 01	0.111	0.162	0.067	0.175	0.017	0.377	-0.006	0.463
12 vs. 02	0.046	0.264	0.031	0.281	0.091	0.162	0.311	0.054
12 vs. 03	0.200	0.080	0.041	0.229	0.309	0.039	0.143	0.132
12 vs. 04	0.169	0.130	-0.015	0.513	0.143	0.145	0.254	0.017
12 vs. 05	0.274	0.030	0.243	0.041	0.322	0.041	0.444	0.004
01 vs. 02	0.022	0.364	0.026	0.314	-0.126	0.968	0.159	0.093
01 vs. 03	-0.019	0.494	0.000	0.439	0.061	0.195	0.035	0.288
01 vs. 04	0.019	0.175	0.009	0.405	0.020	0.335	0.009	0.416
01 vs. 05	0.183	0.082	0.135	0.126	0.200	0.045	0.081	0.162
02 vs. 03	-0.102	0.827	-0.030	0.511	-0.081	0.799	-0.044	0.558
02 vs. 04	0.065	0.223	0.044	0.275	-0.126	0.933	0.243	0.028
02 vs. 05	0.026	0.344	0.111	0.167	0.219	0.028	0.352	0.006
03 vs. 04	0.087	0.229	0.000	0.420	-0.013	0.468	0.030	0.374
03 vs. 05	-0.006	0.483	0.185	0.082	0.430	0.004	0.206	0.026
04 vs. 05	-0.015	0.513	0.143	0.108	0.196	0.058	0.039	0.268

Classification and ordination analyses for the Molenaars reach (Figures 7.3a, b) showed little difference between samples representing the same biotopes in the experimental and control locations; the corresponding ANOSIM provided confirmation (Table 7.6). Highly significant, however, was the clear delineation of biotope types, entirely supported by the ANOSIM results, where maximum biotope differentiation was apparent relative to all other sites (Table 7.6). Pairwise tests indicated that the greatest differentiation of assemblages was apparent for pools and riffles (R = 0.898, *P* = 0.001). Similar, highly significant assemblage differentiation was also obtained between riffles and runs (R = 0.541), and runs and pools (R = 0.532). Natural variability in assemblage composition was markedly higher for pools than the other two biotopes (Figures 7.3a, b). Furthermore, variability also appeared greater for this biotope, as well as for

riffles and runs to a lesser extent, early in the dry season (Dec-Jan: large ordination distances, Figure 7.3b) and in May when discharges were relatively high.

Where pools and runs, or runs and riffles, grouped together, dendrogram sub-clusters remained separate based on biotope and also reflected location pairs (Figure 7.3a). An exception was the grouping of run assemblages impacted by extreme low flows with control pool assemblages in the same month (February), as well as with impacted pool assemblages from both months of the impact phase, at 72% similarity; the pattern was less apparent in the ordination plot (Figure 7.3b). The potential effect appeared to have been entirely lost by March, when control and impact run assemblages were again highly similar. In contrast with pools and runs, impacted riffle fauna grouped closely at high levels of similarity (> 70%) with corresponding control assemblages for both the impact phase and early recovery phase (April), suggesting little direct effect of extreme low flows on riffle composition (Figure 7.3a).

The results of SIMPER analyses for biotopes at the Molenaars site (see Appendix 7.3b, for details) indicated that within-biotope assemblages were typified according to relative abundances of Baetidae, Simuliidae, Acarina, Teloganodidae, Heptageniidae and Chironomidae, with intra-biotope similarity greatest for runs (73%) and riffles (72%), and least for pools (64%). It should be borne in mind that at this site (as at the Du Toits and Riviersonderend sites), SIMPER comparisons incorporate any undetected or subtle effects of extreme low flows (and similarly, season) on assemblage composition for samples representing the impact location midsummer (see Section 7.4.3).

The Simuliidae was the main family responsible for the observed differences between riffles and runs, with 256.9 and 7.3 individuals 0.1 m^{-2}, respectively. An additional six taxa, including Hydraenidae, were also more abundant in riffles than runs (Appendix 7.3b). In contrast, higher densities of Leptoceridae (4.2 cf. 0.9 0.1 m^{-2}), Oligochaeta (8.3 cf. 6.7 0.1 m^{-2}), and Teloganodidae (34.0 cf. 10.1 0.1 m^{-2}), were recorded in runs than riffles, respectively. As was found for the Elands River, the Philopotamidae was a useful discriminator between the two biotopes (mean contribution: SD ratio = 2.34). Pool assemblages differed from both riffles and runs principally in having lower abundances of shared families (Appendix 7.3b). Comparison of riffles and pools demonstrated that of five key taxa, the Simuliidae contributed the most to biotope separation and was a potential indicator family (mean contribution: SD ratio = 2.90); similar ratios were also obtained for Chironomidae and Hydropsychidae. Chironomid abundances were the primary drivers of the separation between run and pool assemblages at this site (190.9 vs. 16.4 individuals 0.1 m^{-2}, respectively), with the highest individual contribution to percentage dissimilarity and ratio of mean contribution to SD (1.86).

Grouping by biotope type was far more pronounced than by season (month), although there was some separation of December samples from those of other months, as well as an apparent higher degree of similarity among assemblages over the February-April period (Figures 7.3a, b). A one-way ANOSIM highlighted the absence of a significant effect of month, on average, for the Molenaars site (Global R =

0.059, $P = 0.140$; Table 7.7). The sole significant difference, between December and May (R = 0.243, $P = 0.041$), was principally a function of lower numbers of baetid mayflies and hydropsychids in May, and the converse for blackflies (Appendix 7.4).

In the case of the Du Toits River, the overall difference in assemblages between locations at the site was minimal, on the basis of classification and ordination (Figure 7.4a, b) and ANOSIM results (Table 7.6). In contrast, the biotope affinities of assemblages were marked (second only to the Molenaars, at R = 0.533, $P = 0.001$), and more developed than those of months (or seasons) (see below). Riffle assemblages were most distinct from those of pools (R = 0.812, $P = 0.001$). Lesser, but still highly significant differentiation of assemblages was obtained for riffles vs. runs (R = 0.485), and runs vs. pools (R = 0.334). Eight taxa were responsible for the internal similarity of each biotope, based on SIMPER analysis (Appendix 7.3c). Riffles and runs showed the greatest internal faunal similarity (73%), with higher natural variability in assemblage composition for pools (67%; see also Figures 7.3a, b).

Riffles in the Du Toits reach were differentiated from runs primarily on the basis of higher numbers of simuliids (696.4 cf. 15.4 0.1 m^{-2}), baetids (267.1 cf. 58.5 0.1 m^{-2}), and chironomids (512.5 cf. 206.9 0.1 m^{-2}). Of these families, the Baetidae emerged as a possible discriminator between the two biotopes (mean contribution: SD ratio = 1.65). Riffles also were characterized by relatively high densities of empidids, water mites, and elmid and hydraenid beetles (Appendix 7.3c). Characteristic of runs, with higher abundances than in riffles, were Teloganodidae (14.3 vs. 3.3 0.1 m^{-2}), Caenidae (3.1 vs. 0.6 0.1 m^{-2}), and Leptophlebiidae (8.3 vs. 4.4 0.1 m^{-2}). Comparison of riffle and pool assemblages again showed simuliids, chironomids and baetids representing the greatest contributors to cumulative dissimilarity (Appendix 7.3c). In addition, caenids were markedly more common in pools than riffles (18.5 cf. 0.6 0.1 m^{-2}), as expected given the habitat requirements of members of this family (Merritt and Cummins 1984; Scholtz and Holm 1985). Water mites and elmids were more abundant in riffles, while empidids were absent in pools. On the basis of mean contribution: SD ratios, the Chironomidae showed most potential as a discriminatory family with a figure of 2.06. Pools exhibited comparatively higher densities of five families than runs (Appendix 7.3c), most notably Caenidae with 18.5 individuals 0.1 m^{-2} in the former instance. As in the case of both other biotopes, Simuliidae contributed the most to the observed dissimilarity among invertebrate assemblages (15.4 vs. 2.1 individuals 0.1 m^{-2} in riffles and pools, respectively). It was again the Chironomidae, however, that showed most discriminatory potential (mean contribution: SD ratio = 1.53).

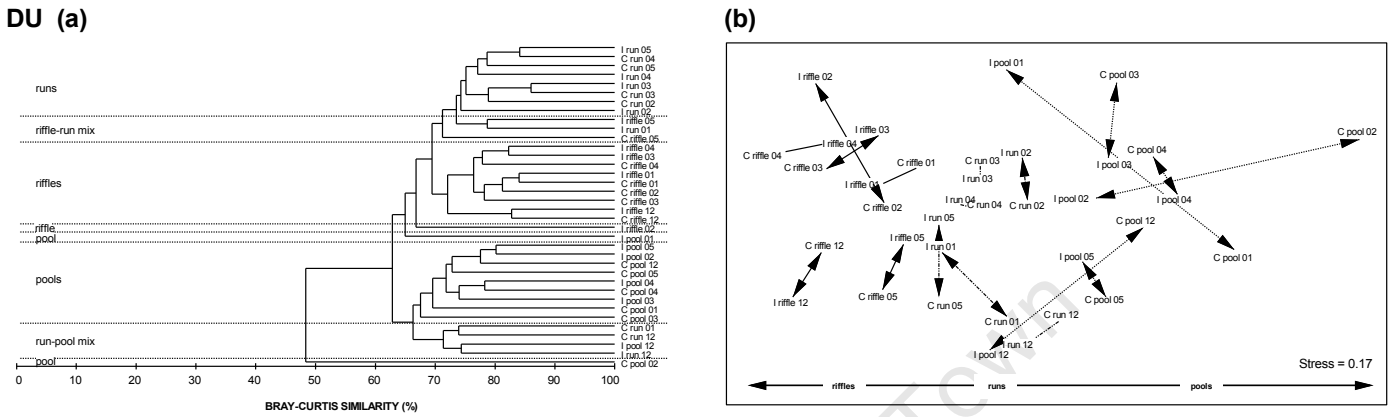


Figure 7.4 **(a) Dendrogram of assemblages from different biotopes (mean family abundances 0.1 m^{-2}) for control (C) and impact (I) locations at the Du Toits site.** 12-05 indicate month (Dec-May). Principal group divisions are demarcated by dotted lines. **(b) Corresponding ordination plot**. Sample pairs are indicated by lines with two-way arrows: riffles (solid), runs (dot-dash), pools (dot).

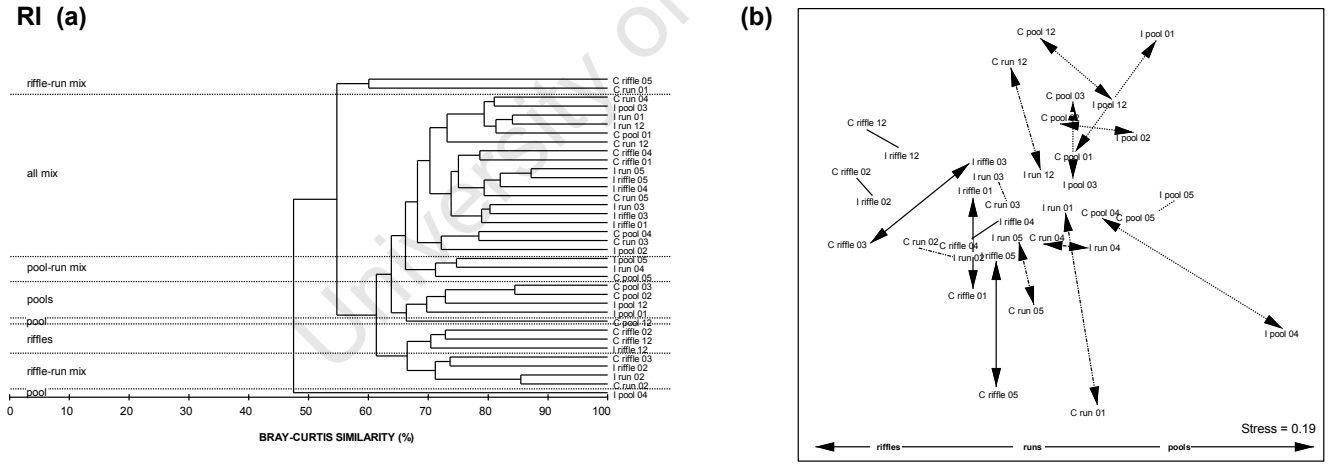


Figure 7.5 **(a) Dendrogram of assemblages from different biotopes (mean family-level abundances 0.1 m^{-2}) for control (C) and impact (I) locations at the Riviersonderend site. (b) Corresponding ordination plot**.

Seasonal influences were overridden by the influence of biotope character, and proved difficult to detect in the above analyses for the Du Toits site. The ANOSIM analysis by month, however, indicated a significant (P = 0.031) overall effect at R = 0.105 (Table 7.7). Pairwise tests showed that the main difference in assemblage composition was between May (reflecting early autumn) and the remaining months, as at the Elands and Molenaars sites, but with a greater divergence in assemblages between the lowest flow periods and months of higher flow (five of 15 pairwise tests were significant; Table 7.7). A SIMPER analysis of the differences in composition of assemblages from early summer and autumn showed primarily that teloganodid numbers were elevated in May, while baetids were in lower numbers than in Dec; the latter represented the singularly consistent difference observed across all sites (Appendix 7.4).

Classification and ordination results for the Riviersonderend site are depicted in Figures 7.5a, b, respectively. They were supported by the ANOSIM results which showed no significant effect for location (Table 7.6). Differentiation of biotope assemblages on the basis of family-level composition was comparatively weak (Figures 7.5a, b), further in evidence in the ANOSIM results (Table 7.6). In particular, run assemblages grouped either with pools or, more commonly, riffles, rather than forming a biotope-specific cluster(s) (Figure 7.5a); ordination results were in agreement (Figure 7.5b). Also, many of the samples representing a combination of all three biotopes ('all mix') grouped fairly tightly at a relatively high similarity (72%), suggesting little difference among biotopes or months (see below for discussion of seasonal influence).

At the Riviersonderend site, within-biotope average similarities were similar at 68% for riffle and run assemblages, and 66% for those of pools; detailed results of the SIMPER biotope analysis are provided in Appendix 7.3d. Runs were distinct from riffles in possessing higher numbers of teloganodids and leptocerids. In contrast, riffles were inhabited by higher numbers of seven dominant taxa (Appendix 7.3d), with chironomids contributing most to the difference (169.4 cf. 103.6 0.1 m^{-2} in riffles and runs, respectively). Riffles had higher abundances than pools of simuliids (19.8 cf. 0.4 0.1 m^{-2}), baetids (83.8 cf. 7.2 0.1 m^{-2}), and elmids (34.7 cf. 4.0 0.1 m^{-2}), in particular, while pools exhibited the highest densities of Teloganodidae (5.2 per 0.1 m^2) and Leptoceridae (16.3 individuals 0.1 m^{-2}) across all biotopes. Notonemourid stoneflies were absent from pools, but present in low densities in riffles and runs. Pools also were characterized by higher numbers than in runs of chironomids, leptocerids and oligochaetes. Runs, in comparison, possessed higher numbers of five other taxa (viz. simuliids, elmids, athericids, hydroptilids, baetids). The Simuliidae exhibited consistently the greatest discriminatory potential across all biotopes, with mean contribution: SD ratios of 1.64 (riffles vs. runs), 2.29 (riffles vs. pools) and 1.66 (runs vs. pools).

There was some evidence of an among-biotope response to extreme flow reduction in the Riviersonderend R. late in the impact phase, with impacted riffles grouping more closely with impacted runs than was apparent under natural flows (Figure 7.5a). The composition of pool assemblages subjected to abnormally low discharges differed markedly from February to March, according to classification results (see also the pool

ANOSIM results for the impact phase, below); ordination results were less convincing (Figures 7.5b). Noteworthy also, was the split between pool fauna immediately following the reinstatement of natural flows in April from the rest of the data set, at only 48% similarity. Although perhaps representing an outlier (divergences also occurred for two control samples at low levels of similarity; Figure 7.5a) earlier findings (Chapters 5 and 6), and further analyses below, pointed to a plausible response (Section 7.8).

There was less evidence of seasonal separation of assemblages from classification and ordination analyses than from the ANOSIM by month for the Riviersonderend R. (Table 7.7), probably due to the strong influence of biotope type (as found for the other sites). Effects of month at this scale were most pronounced of all sites for the Riviersonderend site (Global R = 0.144, P = 0.008). Significant temporal effects on invertebrate assemblages were recorded for five pairs of months (Table 7.7), as at other sites mostly due to a detectable shift in composition from the start to very end of the dry season. Of the families most responsible for the dissimilarity (41%) in December and May (Appendix 7.4), the greatest contribution was a result of lower leptocerid and higher hydroptilid densities in May.

7.4.3 Biotope-specific changes in assemblage composition at lowest flows

Biotope composition at extreme low flows

An ANOSIM analysis focusing on any changes in the invertebrate composition of the main biotopes, defined *a priori*, targeting discharge reduction in the experimental locations mid-summer (Table 7.8), again highlighted natural inter-biotope differences in assemblages ($P \leq 0.002$ across sites) (see Table 7.6). Examination of the control (Elands) data set, through pairwise group tests, showed non-significant assemblage differences between runs and pools mid-summer, for each location (control: $P = 0.147$; impact: $P = 0.340$); both hydraulic biotopes were only moderately differentiated at this site (cf. the river's most similar counterpart, the Molenaars site). Furthermore, greater variability was apparent within the impact location, where biotope character was less well defined for all types (Table 7.8). Even with some within-reach variability at this level of analysis, there still was no significant difference between assemblages from control and impact biotopes of the same type (e.g. low R statistic of 0.002 at $P = 0.403$, for corresponding riffle assemblages). An independent ANOSIM analysis of data for individual impact-phase months showed that for the control-impact pairs, the degree of internal similarity of invertebrate assemblages of all of the biotopes decreased from February to March, as the natural period of low flow disturbance progressed.

At the Molenaars site, all pairwise comparisons were significant (Table 7.8) supporting earlier indications of greatest hydraulic biotope differentiation of all sites for this river (Chapter 6). Most importantly, there was no major effect of a 36% reduction in discharge on biotope invertebrate character, as compared with natural conditions, with all control-impact biotope pairs showing low, non-significant, R values. Independent ANOSIM analyses for the biotopes by impact month, for locations, indicated though that while riffle and pool assemblages showed increasing degrees of divergence in internal composition from February to March, run fauna from different places in the reach became more similar.

Table 7.8 One-way ANOSIM results for individual sites, comparing invertebrate assemblages from different biotopes within the control and impact locations during the impact phase (Feb-Mar). R statistics for pairwise tests of factor groups (biotopes, *n* = 6 per group) are followed by *P* values in parentheses (*significant).

FACTOR SITE	LOCATION BIOTOPE Global R	*P*			PAIRWISE TESTS FOR GROUPS					
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Elands (control)	0.222	*0.002	Control	Riffle						
				Run	0.700 *(0.002)					
				Pool	0.624 *(0.002)	0.124 (0.147)				
			Impact	Riffle	0.002 (0.403)	0.187 (0.074)	0.109 (0.136)			
				Run	0.459 *(0.015)	0.022 (0.340)	-0.017 (0.537)	0.030 (0.314)		
				Pool	0.654 *(0.002)	0.189 *(0.045)	-0.050 (0.690)	0.154 (0.076)	0.030 (0.340)	
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Molenaars	0.444	*0.001	Control	Riffle						
				Run	0.580 *(0.002)					
				Pool	0.900 *(0.002)	0.378 *(0.006)				
			Impact	Riffle	-0.131 (0.944)	0.469 *(0.011)	0.869 *(0.002)			
				Run	0.713 *(0.002)	-0.111 (0.844)	0.283 *(0.013)	0.624 *(0.004)		
				Pool	0.854 *(0.002)	0.330 *(0.002)	-0.009 (0.487)	0.839 *(0.002)	0.244 *(0.019)	
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Du Toits	0.377	*0.001	Control	Riffle						
				Run	0.319 *(0.004)					
				Pool	0.850 *(0.002)	0.463 *(0.009)				
			Impact	Riffle	-0.083 (0.734)	0.306 *(0.011)	0.806 *(0.002)			
				Run	0.357 *(0.017)	0.059 (0.221)	0.437 *(0.006)	0.341 *(0.011)		
				Pool	0.719 *(0.002)	0.313 *(0.011)	0.041 (0.290)	0.680 *(0.002)	0.185 (0.052)	
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Riviersonderend	0.278	*0.001	Control	Riffle						
				Run	0.224 (0.052)					
				Pool	0.776 *(0.002)	0.433 *(0.002)				
			Impact	Riffle	-0.022 (0.567)	-0.019 (0.550)	0.396 *(0.011)			
				Run	0.487 *(0.006)	0.009 (0.422)	0.300 *(0.009)	0.067 (0.221)		
				Pool	0.707 *(0.002)	0.300 *(0.011)	0.198 *(0.043)	0.296 *(0.037)	0.050 (0.271)	

Although the proportion of flow diverted in the Du Toits reach exceeded that of the Molenaars, there remained no conclusive overall difference in riffle, run or pool assemblages from the two locations (Table 7.8). In comparison with the non impacted data set, however, runs and pools became less easy to distinguish on the basis of their assemblages at extreme low flows (R = 0.185, *P* = 0.052). Between-month ANOSIMs revealed that control-impact pairs for all biotopes were far more similar towards the end of the period of extreme low flows than earlier on.

In the case of the Riviersonderend river, of the dominant biotopes riffles and runs had marginally similar assemblages under naturally lowest discharges (R = 0.224, *P* = 0.052; Table 7.8). With extreme discharge reduction in the impact location (> 85% of natural flow), the two biotopes became more similar in benthic composition, suggesting intensification of a natural effect of low flows (R = 0.067, *P* = 0.221). In addition, run assemblages were no longer significantly different from those of pools (R = 0.050, *P* = 0.271), as compared with natural conditions (R = 0.433, *P* = 0.002). Although some effects of flow reduction could be inferred from such results, comparatively low between-biotope differences at site level (Table 7.6) (coupled with the similarity between biotopes observed under natural flows in the control river), arguably diminished its relevance. There was, however, a significant difference between flow-impacted and natural pool assemblages (R = 0.198, *P* = 0.043); such pairwise effects were not found in any other instance (Table 7.8). The difference was largely attributable to marked percentage declines in the abundance of four of five pool-dwelling taxa with abnormal flow reduction (Table 7.9), notably water mites (55.1 cf. 4.5 0.1 m^{-2}) and baetids (21.9 cf. 2.7 0.1 m^{-2}), as well as increases in the prevalence of leptophlebiids. While pool fauna from the control and impact locations became more similar towards the end of summer, run and riffle fauna increasingly diverged (based on separate ANOSIM pairwise tests for Feb and Mar).

Table 7.9 Results of a SIMPER analysis comparing pool assemblages under natural and extreme low flows for the Riviersonderend site. Taxa are listed from greatest to least contribution to dissimilarity (cutoff at ≤ 50%), with the higher abundance for each taxon between groups indicated in bold.

$\bar{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	POOL AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma\bar{\delta}_i$ %
Control and impact pools = 41.9%	**Control**	**Impact**				
Baetidae	**21.93**	2.68	5.28	1.32	12.61	12.61
Acarina	**55.09**	4.52	5.15	1.33	12.31	24.92
Chironomidae	**279.68**	135.06	4.43	1.18	10.59	35.51
Leptophlebiidae	3.27	**4.50**	4.41	1.34	10.54	46.05
Leptoceridae	**9.03**	7.36	3.97	1.08	9.50	55.54

In combination, these results primarily indicate a detectable disturbance effect of extreme low flows on the Riviersonderend fauna at biotope level. Across all sites, it is improbable that the above results are a function of misclassification of assemblages to hydraulic biotopes, given the high classification successes obtained at very low flows (Section 6.3.2).

Within-biotope invertebrate response to flow reduction

The limited evidence of invertebrate response to low flows for assemblages from different biotopes prompted an attempt to detect direct responses at the level of individual sample assemblages during the February to March period of impact, at individual sites. Classification results are presented below for all sites, while corresponding ordinations are given in Appendix 7.5.

For the Elands site, as expected given that assemblages in both locations were under the same low flow conditions (Chapter 4 and Table 7.7), there was an intermixing of samples from locations and months (Figure 7.6). A limited match occurred between the dendrogram and ordination, with the latter plot (Appendix 7.5a) illustrating a tight grouping of most samples supporting poorer differentiation of biotope types mid-summer. Although riffle and pool assemblages did not group, there were numerous instances where those of runs grouped with either riffles (group 9) or pools (e.g. group 4) (Figure 7.6). In many instances, at higher degrees of similarity, far smaller clusters represented individual biotopes, for example, subgroups (i) - runs, and (ii) and (iv) - riffles, in group 9. A single pool outlier split off at a high degree of dissimilarity (73%) from the sample set, primarily due to the absence of 12 families, most notably Teloganodidae and Chironomidae. Separation of some individual riffle samples was also evident. Both results suggested elevated variability within these two biotopes, as compared with runs.

During the impact phase at the Molenaars site, clear separation of biotope types was apparent, though limited overlap between runs and the other two biotopes was again observed (Figure 7.7 and Appendix 7.5b). However, there remained a considerable mix of samples reflecting both natural and manipulated discharges, for example groups 2 and 9. There was greater separation of samples from the two months than for the Elands R. (e.g. groups 3-5, as well as some sub-clusters, such as (i) within group 2). One impacted sample from a pool (group 1) separated off at a low level of similarity (35%), suggesting a possible flow effect. Comparison of the pool assemblage with the remainder of the sample group indicated that it differed mostly as a result of an entire lack of midge larvae (in addition to 11 other families), while other samples possessed on average 128.1 chironomids per 0.1 m^2, as well as high densities of corixids (5.8 0.1 m^{-2}). However, singletons from control pools also were apparent in the Molenaars reach, and pool outliers also occurred at the control site (see above). The results therefore probably highlight more the variability in assemblage composition characterizing pools than any effect of experimental flow reduction.

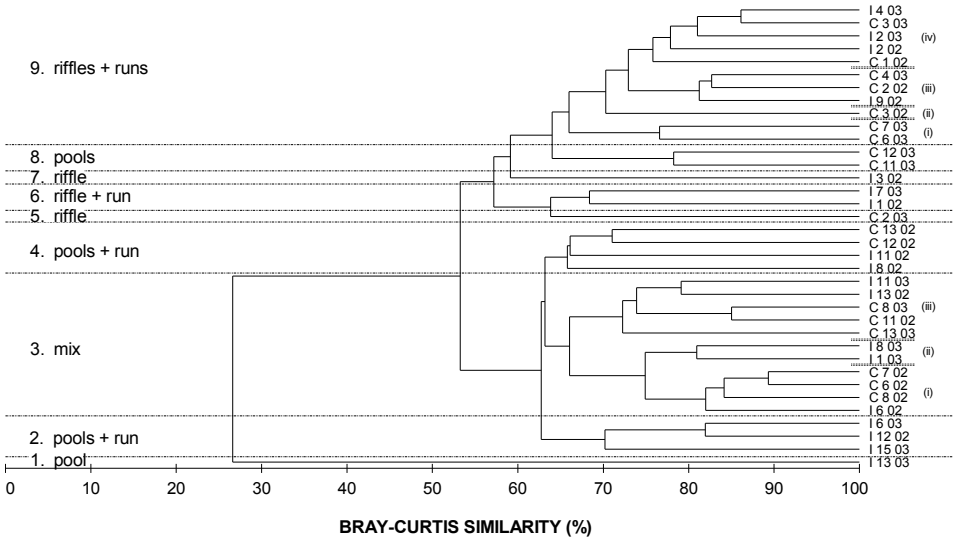


Figure 7.6 Dendrogram of invertebrate samples from different biotopes (family abundances 0.1 m^{-2}) collected from control (C) and impact (I) locations during the impact phase, for the Elands site. Sample numbers (riffles: 1-5; runs: 6-10; pools: 11-15) follow location abbreviations, while 02 and 03 reflect Feb and Mar. Major groups, at highest % dissimilarity, are indicated by dashed lines and numbers 1-9 on the plot left. Select subgroups are demarcated on the right by dividers with numbers in parentheses.

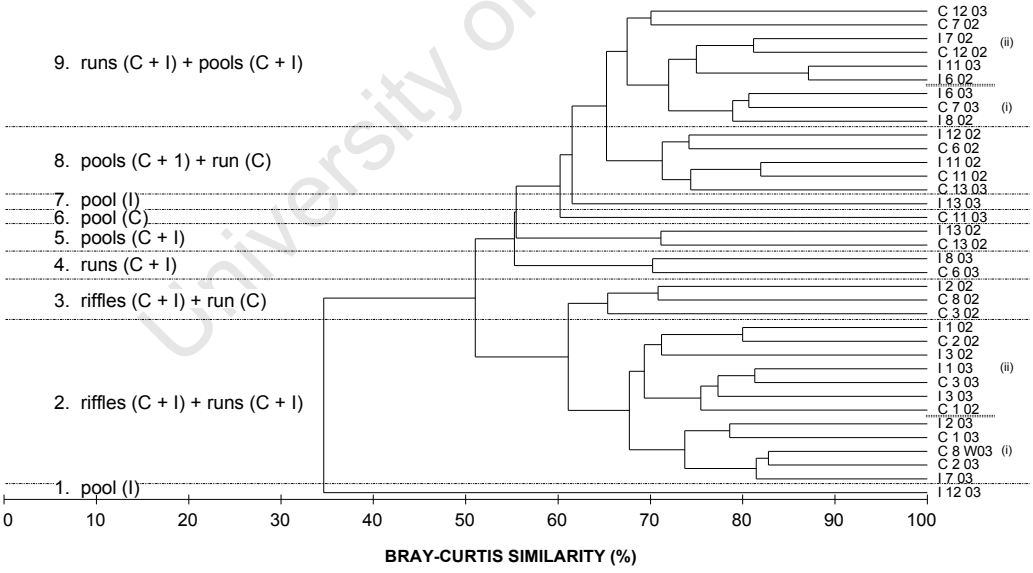


Figure 7.7 Dendrogram of invertebrate samples from different biotopes (family abundances 0.1 m^{-2}) collected from control (C) and impact (I) locations during the impact phase, for the Molenaars site. Sample numbers (riffles: 1-5; runs: 6-10; pools: 11-15) follow location abbreviations, while 02 and 03 reflect Feb and Mar. Major groups, at highest % dissimilarity, are indicated by dashed lines and numbers 1-9 on the plot left. Select subgroups are demarcated on the right by dividers with numbers in parentheses.

Classification results for the Du Toits site (Figure 7.8) show a first separation of a large group of pools (groups 1 and 2) from all other samples, at 46% similarity, with a single flow-impacted sample then splitting from the remainder with which it was still 62% similar (group 1). Ordination results indicated further separation between pool assemblages experiencing natural and abnormal discharges (group 2; see Appendix 7.5c). Analysis using SIMPER, showed that the difference principally was due to far lower densities of caenids (2.0 cf. 13.8 0.1 m^{-2}) and an entire absence of ceratopogonids (cf. 34.9 0.1 m^{-2}) at very low discharges. In addition, riffle-dwelling elmids were encountered in the flow-impacted pools (2.6 0.1 m^{-2}), an atypical family for this biotope under natural circumstances.

Similarly, a response was found for a group of only riffle assemblages, from both locations (group 4), where a flow-impacted sample diverged at 27% dissimilarity (SIMPER results). Greatest cumulative dissimilarity was due to an absence of both water mites and hydroptilids in the impacted riffle assemblage, both taxa being present in densities exceeding 20 individuals per 0.1 m^2 in the other riffle samples. Most marked, however, was the extremely high density of simuliids at 6639.4 0.1 m^{-2} (as compared with fewer than half that number in other samples). Such dense, but still evenly spaced, packing of blackflies on individual stones, beneath extremely thin films of water (mm), was a prominent feature of the very few riffle patches remaining at extreme low flows (pers. obs.). Elmids, a typical riffle-dwelling family were also entirely absent from the sample, as were empidids, while chironomids occurred in lower numbers than in the other samples.

Run assemblages too showed slight low flow influences. Within groups 7 and 8, assemblages from impacted runs were associated with those of riffles from both locations (Figure 7.8 and Appendix 7.5c). This affiliation suggested that at very low flows, runs in some instances resembled riffles on the basis of faunal composition (see also Section 7.5). Comparison of the biota from the impacted runs with the riffle fauna of the same two groups, using SIMPER, revealed that the increased affinity was based primarily on contributions to group similarity of chironomids, baetids and acarinids (taxon relative abundances).

Of further interest was a large cluster, comprising a mix of samples (group 9) at a moderate degree of internal similarity (67%). Closer examination revealed four distinct sub-groups (Figure 7.8). One of these, subgroup (ii), represented an impacted run, while additional impacted run samples, as well as affected pool samples, grouped with control runs in cluster (iii). In combination, these trends indicate some degree of separation of flow-impacted run assemblages from control ones (though not significant on the basis of ANOSIM results - Table 7.8). At extreme low flows, run assemblages transformed to become more like either riffle or pool assemblages. Although these results provided some signal of an effect of extreme low flows, outliers (e.g. group 3) demonstrated that natural variability among samples remained a complicating factor (also apparent in Figure 7.6).

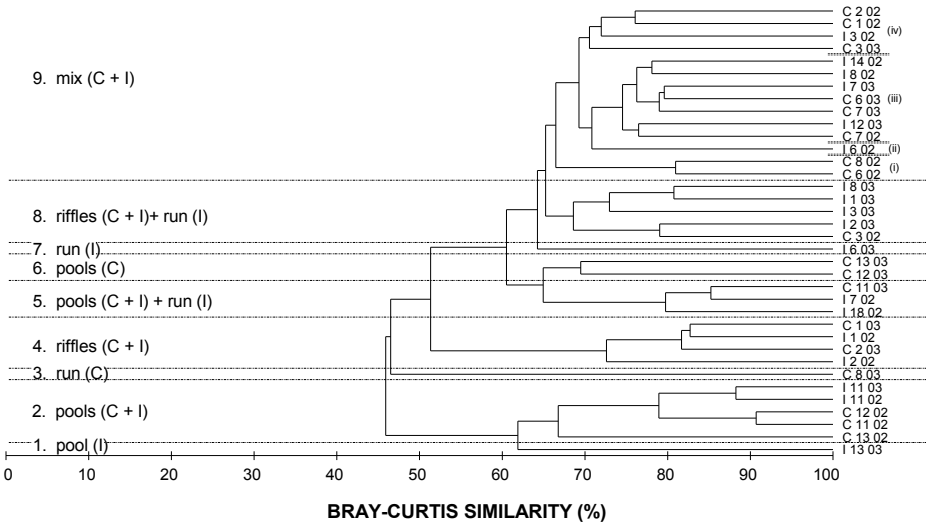


Figure 7.8 Dendrogram of invertebrate samples from different biotopes (family abundances 0.1 m^{-2}) collected from control (C) and impact (I) locations during the impact phase, for the Du Toits site. Sample numbers (riffles: 1-5; runs: 6-10; pools: 11-15 and 18) follow location abbreviations, while 02 and 03 reflect Feb and Mar. Major groups, at highest % dissimilarity, are indicated by dashed lines and numbers 1-9 on the plot left. Select subgroups are demarcated on the right by dividers with numbers in parentheses.

Classification results for the Riviersonderend site are presented in Figure 7.9. There was a notable increase in the separation of samples for this site (though at a high stress level of 0.18, Appendix 7.5d), which contrasted particularly with the control situation (Figure 7.6). There was a greater tendency for riffle and run assemblages experiencing natural discharges to group together than observed at the other experimental sites, while pools showed a natural separation from the other biotopes.

Sample scatter was most apparent for pool assemblages, under conditions of both natural and extreme low flow. Select pool assemblages from the impact location showed an unmistakable response to flow reduction (groups 1 and 2) in both months, but especially in March where they split off at only 45% similarity with all other samples. The dissimilarity was largely a function of an absence of baetids (cf. 63.4 0.1 m^{-2}) and reduction in chironomid abundances in the impacted assemblages, which confirmed earlier findings. However, it should be noted that, as found at the other sites, pool assemblages formed outliers under natural conditions (groups 3 and 6; Figure 7.9).

Though not as an entire group, flow-impacted riffle assemblages also demonstrated some changes in composition, exhibiting a shift away from control riffle samples towards run and even pool assemblages (Figure 7.9). The impacted riffle singly representing group 4 ('I 3 03') separated distinctly from another group of run and riffle samples (group 5), mostly due to an absence of water mites coupled with higher numbers of juvenile (unidentifiable) coleopteran larvae, hydroptilids and veliids than the other samples. Furthermore, within the mix of primarily impacted assemblages comprising group 9 (Figure 7.9), an

impacted riffle sample ('I 1 03') was found to cluster with flow-impacted pools and runs from both locations (sub-group (v)), well removed from the majority of riffle fauna. Sub-group (iii) also represented only impacted samples from all three biotopes. A SIMPER analysis of which families contributed to the collective similarity of all flow-impacted samples in sub-groups (iii)-(v), indicated that their internal similarity (71%) was principally due to their abundances of chironomids and acarinids, in addition to Hydroptilidae, Baetidae, Leptoceridae and Elmidae. These were the only instances across all experimental sites where riffle and pool assemblages grouped closely together. Previous analyses of relative similarity among biotope types had shown no potential for misclassification of pool assemblages with those of riffles (e.g. Table 7.6). The presence of flow-impacted and control riffle assemblages in a single group (sub-group (iii) of group 5; Figure 7.9a), however, supported earlier findings that the observed effects could not be considered the general pattern.

The extent to which the trends discussed above were a function of the hydraulic character of the biotope patches from which samples were taken was demonstrated through BIOENV and other analyses in Section 8.6.

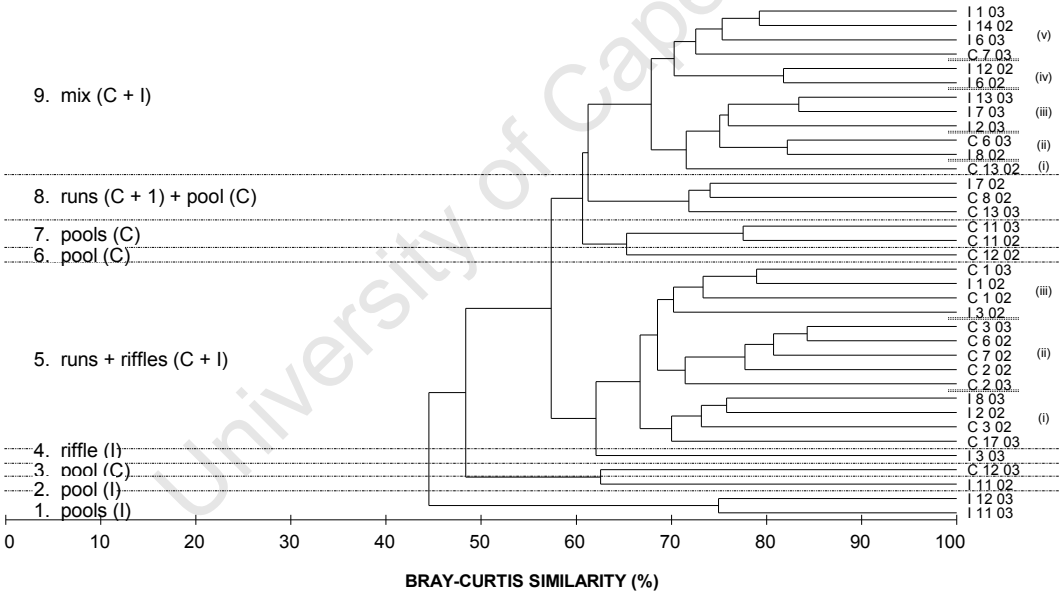


Figure 7.9 Dendrogram of invertebrate samples from different biotopes (family abundances 0.1 m^{-2}) collected from control (C) and impact (I) locations during the impact phase, for the Riviersonderend site. Sample numbers (riffles: 1-5; runs: 6-10 and 17; pools: 11-15) follow location abbreviations, while 02 and 03 reflect Feb and Mar. Major groups, at highest % dissimilarity, are indicated by dashed lines and numbers 1-9 on the plot left. Select subgroups are demarcated on the right by dividers with numbers in parentheses.

7.5 MICRODISTRIBUTION PATTERNS OF INVERTEBRATE ASSEMBLAGES IN RELATION TO LOW FLOW CONDITIONS

7.5.1 Invertebrate assemblage-microhabitat associations at natural and extreme low flows

The finest scale, potential effects of flow disturbance on invertebrates were at the microhabitat level of individual stones, within and among individual biotope patches (riffles and runs, but not pools).

Invertebrate microdistributions at natural low flows

Analyses of variance for numbers of taxa and total numbers of individuals for the components of stone microhabitat sampled, namely stone tops, bottoms, and the substratum underlying each stone (Figure 3.10, Section 3.5), yielded highly significant differences in invertebrate assemblage microdistributions under natural low flows, irrespective of month (and hence, indirectly, flow regime) or biotope type (Table 7.10). Assemblages from all microhabitat components differed significantly from one another (Tukey Unequal n HSD tests). Both numbers of families and total numbers of individuals were greater for the underlying substratum than for stone bottoms, while tops exhibited the lowest values.

Table 7.10 Microdistribution of invertebrates based on ANOVA analyses for numbers of taxa (S) and total numbers of individuals (*N*) (0.1 m^{-2}). Samples were pooled across sites and months for stone tops, bottoms, and underlying substratum (collected only in Dec, Feb, Apr).

VARIABLE	*F*	*P*	MEAN ± STANDARD DEVIATION (no. of samples)		
			Tops	Bottoms	Underneath
S	263.545	*0.000	5.1 ± 2.5 (432)	8.6 ± 3.8 (432)	12.2 ± 4.5 (144)
N	19.6627	*0.000	430.9 ± 849.2 (432)	630.0 ± 875.3 (432)	975.5 ± 1189.9 (144)

As envisaged based on inter-biotope trends in diversity (Section 7.6), at natural low flows both the numbers of taxa and total densities were higher for riffles than runs, for all microhabitats (Table 7.11). Paired t-tests showed that between-biotope differences were significant, except in the case of total numbers of invertebrates for the underlying cobble-gravel (t-value = 1.577, P = 0.118). With the inclusion of the low flow-impacted samples, however, the difference between biotopes for numbers in the underlying substratum was significant (t-value = 2.891, P = 0.004), providing a first intimation of movement of animals from surface stones into underlying bed materials.

Table 7.11 Microdistributions of invertebrates in riffles and runs based on paired t-tests for numbers of taxa and total numbers of individuals (0.1 m^{-2}). Using only samples subjected to natural discharges, samples were pooled across sites and months for stone tops, bottoms, and underlying substratum (collected only in Dec, Feb, Apr). No. of samples = 54 in all cases.

VARIABLE AND MICROHABITAT COMPONENT	t-value	DF	*P*	MEAN ± STANDARD DEVIATION	
				RIFFLES	RUNS
No. of taxa					
Tops	3.177	106	*0.002	6.1 ± 2.8	4.6 ± 2.1
Bottoms	4.585	106	*<< 0.001	12.1 ± 4.0	8.8 ± 3.5
Underneath	2.270	106	*0.025	13.2 ± 4.1	11.2 ± 4.7
No. of individuals					
Tops	3.663	106	*< 0.001	706.1 ± 1011.8	188.3 ± 234.6
Bottoms	4.198	106	*<< 0.001	1402.6 ± 1126.3	592.8 ± 861.1
Underneath	1.577	106	0.118	1061.0 ± 1119.0	721.4 ± 1119.3

Comparisons of microdistributions in terms of taxon numbers and invertebrate densities for control and impact locations, during February (biotopes combined) for only experimental sites, revealed no evidence of significant effects of abnormal flow reduction, for stone tops, bottoms or the underlying substratum (paired t-tests; $P \leq 0.050$). Similarly, analyses independently examining riffle and run assemblages revealed no significant flow-related effects for either diversity index (paired t-tests; $P \leq 0.050$). However, there were detectable shifts in invertebrate microdistributions from those observed under naturally low flows. For riffle microhabitats the numbers of families on stone tops and bottoms declined, and concomitant increases in taxon numbers occurred deeper in the substratum. Conversely, densities of riffle dwellers increased for all microhabitats. In comparison, in runs, both the numbers of taxa and individuals increased on stone tops. Numbers of taxa and individuals also increased in the underlying substratum of run areas, while they decreased on stone undersides.

Patterns of assemblage microdistribution at extreme low flows

Direct, flow-related responses in invertebrate assemblage composition at microhabitat scale, immediately following flow reduction in February, were explored. Based on earlier results (Sections 7.3 and 7.4), biotopes were treated separately, for individual sites. Figure 7.10a presents the resultant ordination plot for the Elands reach, for comparison with plots for the experimental sites, depicted in Figures 7.10b-d; dendrograms closely matched the ordination results. The results of ANOSIMs for comparisons of assemblages from various microhabitat components (regardless of biotope type or low flow pattern) are presented in Table 7.12.

As shown in Figure 7.10a (with omission of a run outlier sample from which invertebrates were absent), and supported by the ANOSIM results (Table 7.12), at the Elands site stone-top assemblages of riffles and runs tended to split off separately from other sample parts (at only 34% Bray-Curtis similarity). A second, lesser

axis of separation between riffle and run top-assemblages was also apparent. Limited separation of assemblages from the two biotopes occurred within the other major cluster that comprised assemblages inhabiting stone bottoms and the underlying substratum.

At the Molenaars site, a single flow-impacted assemblage (a run top) split at a low similarity of 34% from all other samples (Figure 7.10b). The second major division reflected the clustering of all remaining assemblages representing stone tops separately from those from other microhabitat parts (see also the ANOSIM results given in Table 7.12). One impacted assemblage from the top of a riffle stone clustered with both control and impacted run-top assemblages, also providing evidence of a possible flow-related effect. For the second large cluster, there was a noticeable separation of riffle and run fauna that substantiated previous findings. There was no apparent effect of extreme low flows on invertebrate assemblages occupying the underlying substratum. However, as for top assemblages, sample groupings for stone bottoms and the underlying bed indicated a tendency for impacted riffle assemblages to become more similar in composition to those characteristic of runs (see above and Section 7.4.3).

The majority of assemblages inhabiting stone tops in the Du Toits reach separated from those inhabiting the other two microhabitat components, at only 44% similarity (Figure 7.10c); ANOSIM results supported the basic division (Table 7.12). Within one of the two large clusters generated, a single flow-impacted run top was found to group tightly with several run bottom-assemblages. In the other cluster, impacted riffle taxa from stone bottoms were more similar to those of tops than at natural discharges. The 86% reduction in discharge below natural magnitudes also resulted in a sub-cluster, separating at 50% similarity, grouping an assemblage from the top of an impacted riffle stone with control assemblages representing tops of run stones. Some separation of assemblages from impacted run and riffle 'B' and 'U' assemblages, from those of controls was apparent. Greatest divergence between assemblages of stone bottoms and the substratum below them was evident at this site ($R = 0.168$, $P = 0.002$; Table 7.12), possibly largely attributable to impacted bottom assemblages (Figure 7.10c).

In contrast with the other sites, the Riviersonderend reach exhibited a pronounced sample mix, without a major division between assemblages from stone tops and those of other microhabitat components (Figure 7.10d cf. Figures 7.10b, c; Table 7.12). Comparative ANOSIM results highlighted this finding, with lowest R values overall of 0.113 ($P = 0.045$) and 0.325 ($P = 0.001$) for pairwise tests for stone tops versus bottoms, and the underlying substratum, respectively. The majority of impacted run assemblages, from all microhabitat components, as well as one impacted riffle top, split off from the remaining samples at 51% similarity, reflecting an influence of abnormally reduced discharge at this scale. Although the remaining impacted riffle assemblages clustered with those of both control riffles and runs, the pattern is possibly more an effect of the high overlap in character of the two biotopes (Table 7.6) than the low flow treatment.

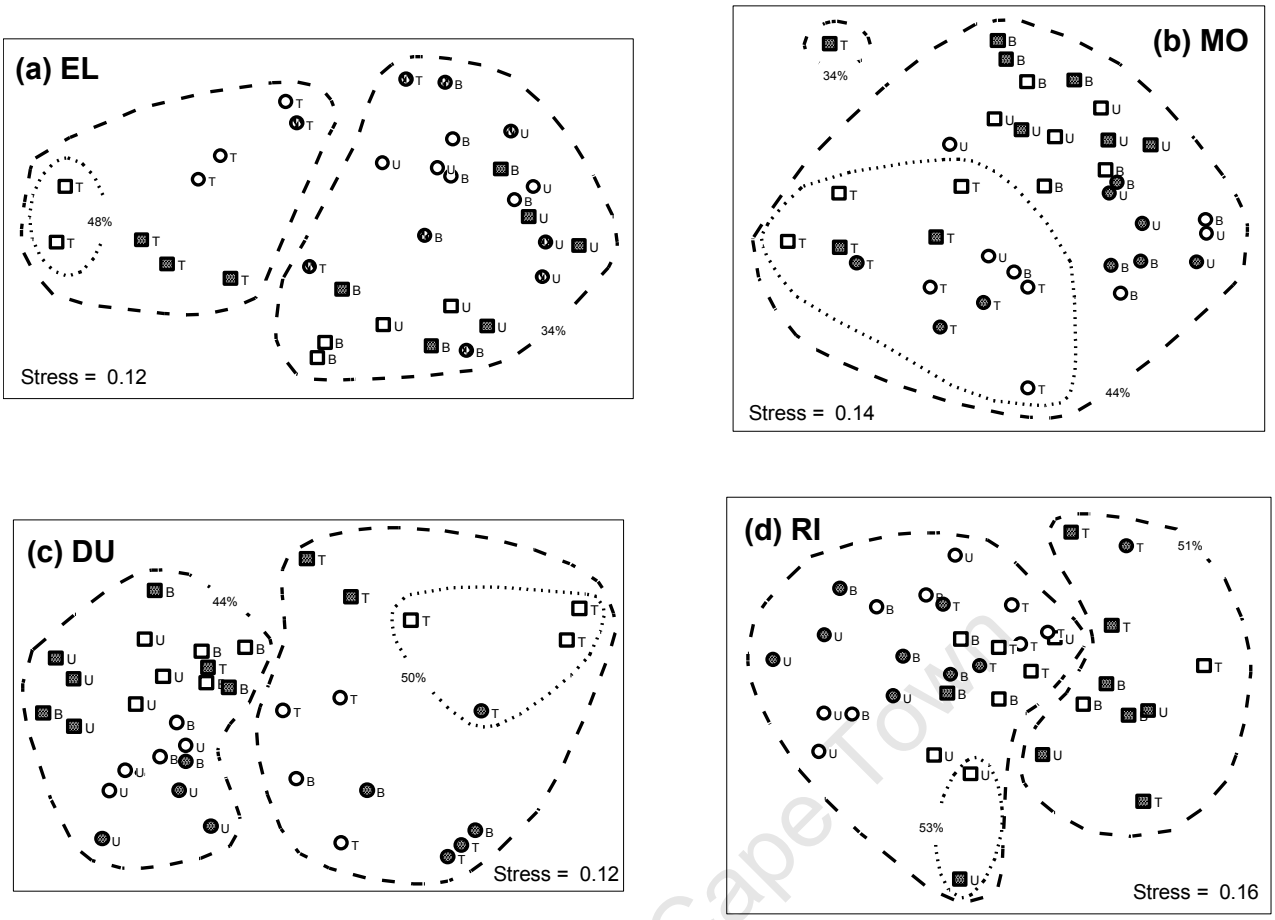


Figure 7.10 Ordination plots showing invertebrate microdistribution patterns for riffles and runs in February, for the individual sites. (a) EL - Elands (outlier excluded); (b) MO - Molenaars; (c) DU - Du Toits; (d) RI - Riviersonderend. Primary (dashed line) and secondary (dotted line) groups from corresponding dendrograms are superimposed, along with the Bray-Curtis similarities for each division. Symbols: control location (open symbols); impact location (solid symbols); riffles (circles); runs (squares); T - stone tops; B - stone bottoms; U - underlying substratum.

Table 7.12 Results of site-specific ANOSIMs comparing the microdistributions of invertebrate assemblages, based on impact phase (February) samples for individual sites. Stone microhabitats: T - tops; B - bottoms; U - underlying substratum. Significant results are shaded.

FACTOR AND SITES	GLOBAL TEST		PAIRWISE TESTS FOR GROUPS R (*P*)		
	R	*P*	T vs. B	T vs. U	B vs. U
Elands	0.479	0.001	0.586 (0.001)	0.769 (0.001)	0.084 (0.122)
Molenaars	0.394	0.001	0.517 (0.001)	0.606 (0.001)	0.041 (0.195)
Du Toits	0.367	0.001	0.268 (0.004)	0.685 (0.001)	0.168 (0.002)
Riviersonderend	0.188	0.002	0.113 (0.045)	0.325 (0.001)	0.139 (0.043)

Although patterns of assemblage microdistribution were complex at all sites, they were unified in exhibiting a significant difference between assemblages inhabiting the tops of stones, from those of the other two

components of microhabitat; this feature was more prevalent than grouping by biotope type. A SIMPER analysis indicated that assemblages from stone tops characteristically had lower abundances (or sometimes zero counts) for some 15 taxa, most commonly Teloganodidae, acarinids and chironomids (others included Heptageniidae, Leptophlebiidae, Leptoceridae, Elmidae and oligochaetes), than those of other microhabitat components. Top assemblages were also typified by greater numbers of Simuliidae and, to a lesser extent, Baetidae, though not consistently.

7.6 GENERAL PATTERNS OF DIVERSITY OF INVERTEBRATE ASSEMBLAGES AMONG BIOTOPES AT LOW FLOWS

Natural differences in assemblage composition among the rivers made it necessary to examine dry-season trends in univariate diversity measures (Section 3.5.2) largely from site-specific to finer scales. Although the Elands represented the only site under an entirely natural discharge regime, its use as a control was limited given such inter-site variations in the numbers of families and their relative abundances. *Post hoc* Dunnett's tests (Zar 1984; StatSoft 2001), with the Elands River was used as a control against which diversity indices at other sites were compared, demonstrated that natural differences in the character of individual sites led to outcomes that were more a function of those differences than low flows. Patterns for individual diversity indices under low flow regimes were examined firstly by assessing the effects of month and hence, indirectly, discharge (Section 8.5 provides complementary analyses of direct discharge magnitude-diversity relationships), location and their interaction using two-way ANOVAs for assemblages from all biotopes combined, with the results presented in Table 7.13. Results of *post hoc* Tukey HSD tests, indicating which months and location pairs were responsible for significant differences, are provided on the corresponding time series plots for individual diversity indices (see Appendix 7.6a-e). Monthly summary statistics for these diversity indices for the main biotopes, for locations at each site, are provided in Appendix 7.7.

7.6.1 Relationships between numbers of taxa, biotope type and low flow regime

Spatiotemporal patterns in numbers of taxa with low flow regime

Across all sites, average, minimum and maximum numbers of invertebrate taxa were similar, with an overall range from one (pool, May), at the Du Toits site, to a high of 23, in the Elands reach (riffle, December) (Appendix 7.6a). Taxon numbers remained stable over site low flow regimes, relative to other diversity measures such as abundance, with no significant effect of month, location or their interaction for any site except the Riviersonderend (Table 7.13). For the last site, the effect observed was seasonal ($F_{5, 96} = 3.472$, $P = 0.006$), a result of higher average family numbers in early summer (December: *c.* ten families) than in other months (especially towards summer's end, when means fell to around six taxa). For the experimental sites, taxon numbers were consistently marginally lower for flow-impacted assemblages than controls, from February to March (while starting off comparatively higher in the preceding month - January cf. February to March; Appendix 7.6a). No relationship was detected between the proportions by which flow was reduced below normal magnitudes and the diversity index.

Table 7.13 **Results of ANOVAs examining the effect of month (discharge), location and their interaction on diversity indices for individual sites.** EL - Elands; MO - Molenaars; DU - Du Toits; RI - Riviersonderend. *S* - total number of taxa; *N* - total number of individuals; *d* - family/higher taxon richness; *J'* - evenness; *H'* - Shannon-Wiener diversity. DF - degrees of freedom (identical for all indices); MS - mean squares. Significant results are shaded. [KW] indicates non-concurrence with a matching Kruskal-Wallis ANOVA by ranks test for month or location. *Post hoc* Tukey HSD results are indicated on the corresponding diversity time series for sites (Appendix 7.6a-e).

SITE AND EFFECT	DF effect	S			N			d			J'			H'		
		MS effect	F	P	MS effect	F	P	MS effect	F	P	MS effect	F	P	MS effect	F	P
EL																
Month	5	9.170	0.684	0.637	567016	4.872	<< 0.001	0.098	0.318	0.901	0.132	6.429	<< 0.001	0.386	3.287	0.009
Location	1	21.333	1.591	0.210	289604	2.488	0.118	0.057	0.183	0.670	0.072	3.525	0.063	0.210	1.793	0.184
Interaction	5	29.044	2.166	0.064	97815	0.841	0.524	0.697	2.258	0.055	0.014	0.668	0.649	0.183	1.558	0.179
Error DF and MS	96	13.410			116383			0.309			0.020			0.117		
MO																
Month	5	5.630	0.399	0.848	2703277	4.836	< 0.001	0.446	1.781	0.124	0.109	8.156	<< 0.001	0.667	7.106	<< 0.001
Location	1	0.750	0.053	0.818	17814	0.032	0.859	0.009	0.038	0.847	0.077	5.748	[KW] 0.018	0.199	2.124	0.148
Interaction	5	10.910	0.773	0.572	207932	0.372	0.867	0.386	1.541	0.184	0.017	1.283	0.277	0.133	1.413	0.227
Error DF and MS	96	14.110			558972			0.250			0.013			0.094		
DU																
Month	5	28.640	2.040	0.080	664089	0.503	0.774	0.745	2.113	[KW] 0.070	0.037	1.337	0.255	0.059	0.366	0.871
Location	1	0.590	0.042	0.838	1001227	0.758	0.386	0.324	0.917	0.341	0.134	4.863	[KW] 0.030	0.403	2.520	0.116
Interaction	5	16.730	1.191	0.319	2020771	1.529	0.188	0.366	1.038	0.400	0.012	0.440	0.820	0.117	0.729	0.603
Error DF and MS	96	14.040			1321485			0.353			0.028			0.160		
RI																
Month	5	28.970	3.472	0.006	212467	5.894	<< 0.001	0.986	4.402	0.001	0.042	1.603	0.166	0.214	1.680	0.147
Location	1	0.037	0.004	0.947	1656	0.046	0.831	0.008	0.034	0.853	0.035	1.338	0.250	0.039	0.303	0.583
Interaction	5	2.770	0.332	0.893	97285	2.699	0.025	0.065	0.289	0.918	0.045	1.742	0.132	0.107	0.843	0.522
Error DF and MS	96	8.345			36048			0.224			0.026			0.127		

Numbers of taxa associated with different biotope types at low flows

Variability in the average numbers of taxa inhabiting different biotopes across months and locations was moderate for all sites, with few obvious trends in relation to season or extreme flow reduction (Appendix 7.7). In the latter case, relative shifts in numbers per biotope from January to February, for control versus impact locations, were inconsistent among sites, including the control site, rendering detection of change complex.

Riffle, run and pool biotopes exhibited significant differences in the numbers of taxa inhabiting each of them under natural flow conditions (single-factor ANOVA: $F_{2, 213} = 17.262$, $P = 0.000$; control data sets pooled), with riffle values significantly elevated above those of runs (Tukey HSD test, $P = 0.014$) and runs above pools ($P = 0.006$) (Figure 7.11). Highest numbers of taxa were recorded for riffles at all sites, with a $mean_{max}$ of 19.0 at the Du Toits (Dec) and a $mean_{min}$ of 4.7 families for the Riviersonderend (May), generally followed by runs, and then pools (Figure 7.11 and Appendix 7.7). The difference among biotopes was, however, sometimes slight in a particular month (e.g. Molenaars River, December).

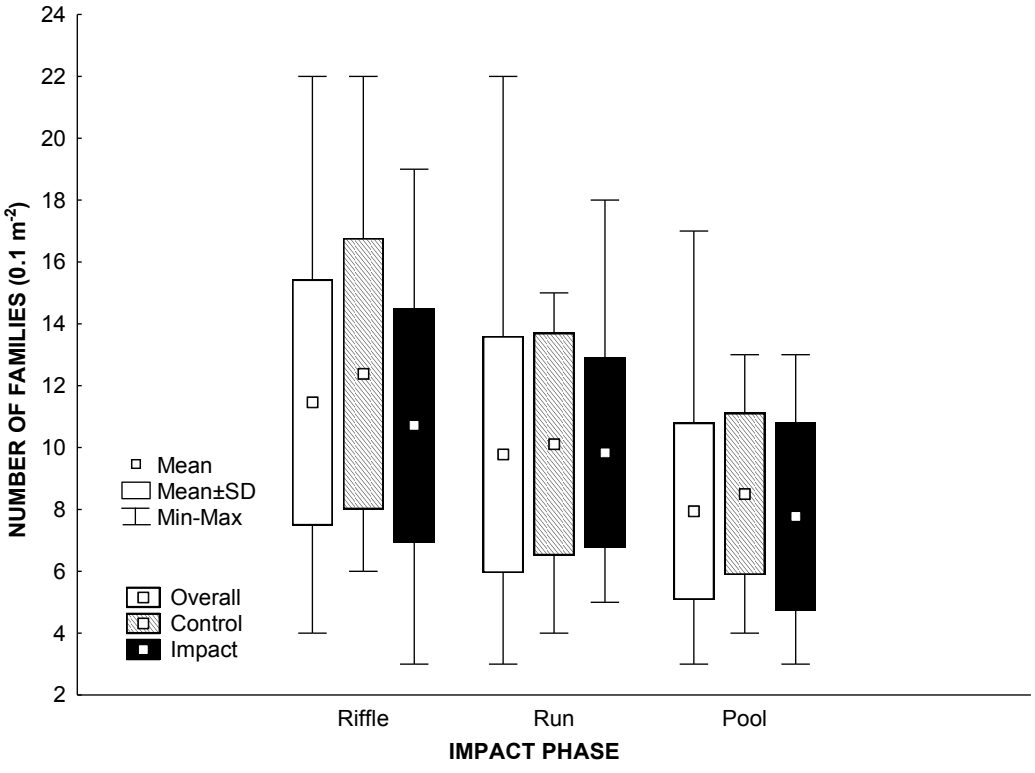


Figure 7.11 Statistical distribution of numbers of families recorded for invertebrate assemblages from different hydraulic biotopes. Numbers of families reflecting natural flow conditions for the study duration ('Overall', Dec-May), pooled from all sites, are contrasted with both control and impact values for the impact phase (Feb-Mar), for only the three experimental sites. 'Impact' represents all assemblages potentially impacted by discharge reduction below natural Q_{min}.

Although the same relative trend was exhibited among biotopes when exclusively considering the peak of the dry season (Feb-Mar), for assemblages at naturally lowest discharges, mean values were marginally higher and the only significant pairwise difference was a higher number of families in riffles ($\bar{x}$ = 12.4) than in pools ($\bar{x}$ = 8.5) (P = 0.006); runs exhibited intermediate values (Figure 7.11). For the combined flow-impacted data set (Section 3.5.1), over the same months, mean S values were lower than under natural flows for all biotopes, especially for riffle-dwelling assemblages ($\bar{x}_{control}$ = 12.4 ± 4.4 versus $\bar{x}_{impact}$ = 10.7 ± 3.8; Figure 7.11). None of the differences was significant (paired t-test results - Table 7.14). *Post-hoc* tests showed less divergence among biotope types than for the control situation, though the significant difference between riffle and pool taxon numbers remained (P = 0.028).

Table 7.14 Results of t-tests for comparisons of diversity indices for individual biotopes, for control and impact locations during the impact phase (February-March). Data were pooled from only the experimental sites (Molenaars; Du Toits; Riviersonderend), for each location, with the impact location assemblages potentially impacted by discharge reduction to varying degrees below natural Q_{min}. For all tests: sample n = 18 for each location, DF = 34. A single significant result is shaded.

BIOTOPE	NO. OF TAXA		NO. OF INDIVIDUALS		RICHNESS		*E*VENNESS		DIVERSITY	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Riffle	1.221	0.230	-0.191	0.850	1.166	0.252	1.192	0.242	1.208	0.235
Run	0.249	0.805	-0.545	0.589	0.424	0.674	0.273	0.787	-0.134	0.894
Pool	0.764	0.450	2.088	0.044	0.275	0.785	-0.558	0.580	0.093	0.926

7.6.2 Relationships between invertebrate abundances, biotope type and low flow regime

Spatiotemporal fluctuations in total numbers of individuals

Wide fluctuations in total invertebrate abundances were recorded between locations and over time at each site (Appendix 7.6b), despite general recognition of the low flow period as stable. Moreover, there were clear differences in abundances among sites, with the Riviersonderend possessing far lower numbers of individuals. Overall, mean numbers of individuals ranged from 8.2 0.1 m^{-2} (Jan, Riviersonderend) to a maximum of 7181.5 0.1 m^{-2} (Mar, Du Toits). There were highly significant seasonal effects ('month') at all sites except the Du Toits, where variability among individual samples masked any such effect (Table 7.13). Similar temporal patterns in abundance occurred at the Elands and Molenaars sites, with elevated numbers early and, in particular, late in the dry season when compared with midsummer. The pattern was not the same for the other sites, where elevated abundances were recorded, albeit sporadically, in midsummer. Mean invertebrate densities were the highest (and most variable) overall for the flow-impacted section of the Du Toits River, immediately after flow diversion, mostly attributable to large numbers of riffle-dwellers (Appendix 7.7). Later during the impact phase, the converse pattern was evident, with densities dropping off rapidly. In the Riviersonderend River, abundances diverged most significantly between February and late

summer (Tukey HSD results - Appendix 7.6b). The interaction of month with location was found to be significant only at the Riviersonderend site ($F_{5, 96}$ = 2.699, P = 0.025; Table 7.14), but Tukey HSD results revealed that it was not a function of flow diversion (Appendix 7.6b).

Numbers of individuals associated with different biotope types at low flows

As in the case of taxon numbers above, comparisons of mean numbers of individuals for various biotopes showed little consistency in the timing of lowest or highest figures from Dec-May, at individual sites (Appendix 7.7). Under a natural low flow regime, significant inter-biotope differences in numbers of individuals were observed, for all sites in combination (single-factor ANOVA: $F_{2, 213}$ = 25.549, P = 0.000). Tukey HSD tests showed that this was attributable to significantly higher densities in riffles than in runs (P << 0.001) and pools (P << 0.001) (Figure 7.12). Abundances in runs and pools did not differ significantly overall (P = 0.615); although pools typically were inhabited by fewer individuals than runs, runs occasionally had lower invertebrate numbers (Appendix 7.7).

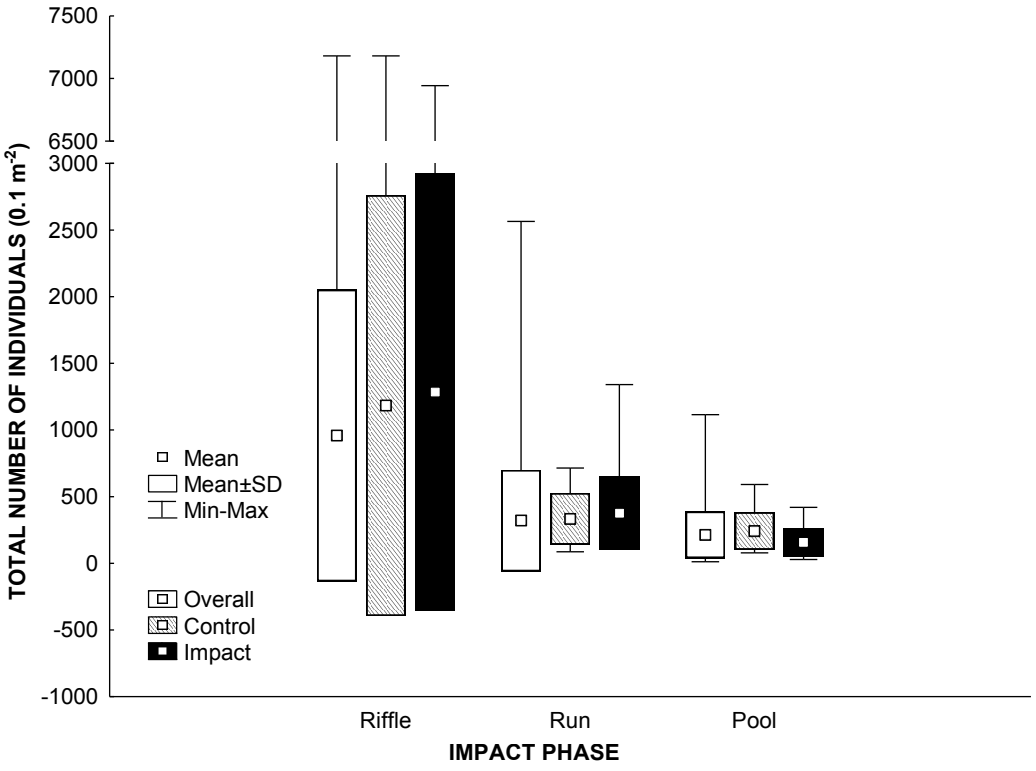


Figure 7.12 Statistical distribution of total numbers of individuals for invertebrate assemblages from different biotopes.

At naturally low flows in midsummer, the difference between runs and pools further diminished. Riffle inhabitants remained at significantly higher numbers ($\bar{x}$ = 1183.3) than in runs ($\bar{x}$ = 333.6, P = 0.021) or pools (P = 0.010) (Figure 7.12). Considering the aggregated flow-impacted data for the same period, the relative inter-biotope differences found for natural low flows persisted. Mean abundances were marginally

above natural, however, for both riffles and runs (Figure 7.12). Pool densities showed a distinct inverse trend (impact $\bar{x}$ = 157.2 cf. control $\bar{x}$ = 242.9), which was the only significant response to extreme low flows for any diversity index for any biotope (t-value = 2.088, P = 0.044; Table 7.14).

In terms of detectable, site-specific shifts in individual biotopes, from pre- to during-impact, within the Du Toits flow-impacted location, riffle numbers increased as pools lost individuals (1541.4 individuals in Jan to only 224.1 in Feb; Appendix 7.7). Mean pool abundances in the flow-impacted location of the Riviersonderend declined noticeably from pre-impact to February, by 58%, compared with a natural increase. In contrast, in riffles at extreme low flows the natural trend was amplified, with highest mean and maximum numbers of individuals recorded in February ($\bar{x}$ = 791.8 ± 367.5 and 1158.2 individuals 0.1 m^{-2}, respectively). Within the Molenaars impact location, however, densities of riffle invertebrates decreased by 59% from January to February, while those of pools more than doubled.

7.6.3 Dynamics in family richness with low flow regime and biotope type

Spatial and temporal patterns in family richness at low flows

Two-way ANOVA results yielded only a single highly significant effect on taxon richness, for the Riviersonderend site, for month, ($F_{5, 96}$ = 4.402, P = 0.001; Table 7.13), due to December exhibiting significantly higher *d* values than other months (Appendix 7.6c). Additionally, the only significant pairwise difference, again for this site, reflected the decline in average richness from 1.917 (Dec, control) to 1.149 (May, impact). Family richness was stable in all other instances across sites, as envisaged given trends for numbers of taxa and relationship between these two indices (Appendices 7.6a, c). Although differences in richness between location pairs in any month were low in most instances, the greatest difference in means for a site was actually recorded for the Elands River at natural low flows (Mar, Appendix 7.6c). Overall, taxon richness ranged from virtually nil (a single pool taxon) to a sample maximum of 3.667 (run sample), both in the Du Toits reach in May.

At the Molenaars site, for the duration of flow diversion as well as in the month following the reinstatement of natural flow, taxon richness was lower (though not significantly so) than at other times; this represented a switch in pattern from typically higher values than the control location at natural flows (Appendix 7.6c). Lower values midsummer (Feb-Mar) were also recorded in the flow-impacted section of the Du Toits reach, including the site $mean_{min}$ of 1.573. In contrast, no such trend in mean values was apparent for the Riviersonderend impact location, although the site minimum *d* (0.348) was recorded there, for a pool in February.

Variations in family richness associated with different biotopes at low flows

Comparisons of average family richness for various biotopes showed a lack of regularity in the time of lowest or highest *d* across sites and biotope types (Appendix 7.7). With extreme discharge reduction, in the

Molenaars reach, riffle assemblages showed the same tendency as natural (i.e. an increase), though stronger, from January to February. The converse trend from natural, of a decline for runs (notably in Feb: $\bar{x}_{control}$ = 2.132 cf. $\bar{x}_{impact}$ = 1.440) was observed, however, mimicking overall patterns of change (Appendix 7.6c). Also, although *d* increased naturally from January through to March, for pools subjected to extreme low flows in March mean richness remained lower than in the control location. For the Du Toits site, a decrease in riffle richness was noted, when compared with the natural direction of response from early to midsummer. More apparent, was an increase in pool taxon richness at very low discharges in February ($\bar{x}_{control}$ = 1.228 cf. $\bar{x}_{impact}$ = 1.909). No distinct responses were evident for the Riviersonderend reach.

The significant inter-biotope differences in taxon richness obtained for all sites in combination, for the whole dry season (control data, single-factor ANOVA: $F_{2, 213} = 5.315$, $P = 0.006$), were entirely due to pools showing lower mean values than both riffles ($P = 0.014$) and runs ($P = 0.012$) (Tukey HSD tests; Figure 7.13). Richness was highly similar between riffle and run assemblages, a somewhat surprising result given the significant differences in family numbers (Section 7.6.1). With a natural decrease in discharge midsummer, the differences in richness across biotopes were no longer significant, with increased *d* values in all cases (Figure 7.13). With extreme flow reduction, richness was marginally reduced in all biotopes (mean *d* range: 1.378, pools - 1.529, runs), though with far lower riffle minima (cf. control; Figure 7.13). However, such shifts were not significant (Table 7.14), and included increasing uniformity between riffle and run assemblage richness.

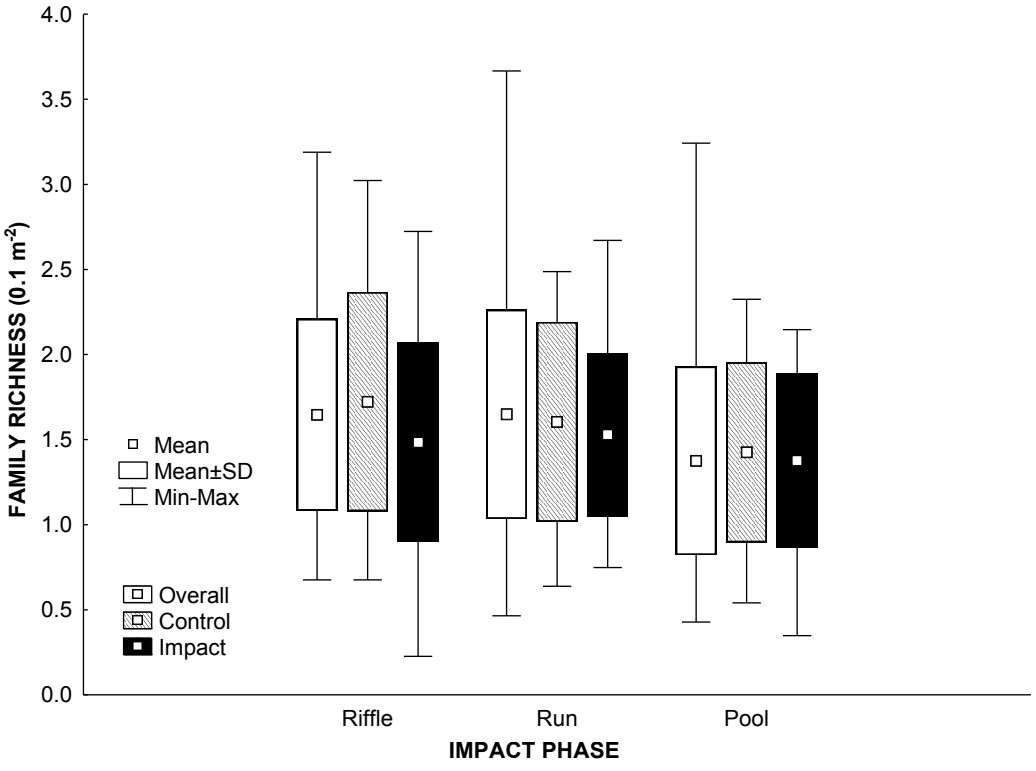


Figure 7.13 Statistical distribution of family-level richness for invertebrate assemblages from different biotopes.

7.6.4 Changes in assemblage evenness with low flow regime and among biotopes

Spatiotemporal patterns in family-level evenness

Site-specific changes in family evenness (and hence, shifts in dominance) with fluctuations in low flow regime over time are depicted in Appendix 7.6d. Both absolute minimum and maximum evenness (and diversity - see below) were recorded in the Du Toits reach, in pools; the former value was effectively nil due to the presence of a single family in a sample. Significantly high temporal variations in assemblage evenness with discharge regime were evident at both the Elands ($F_{5, 96} = 6.429$, $P << 0.001$) and Molenaars ($F_{5, 96} = 8.156$, $P << 0.001$) sites over the dry season (Table 7.13 and Appendix 7.6d). At both sites, $mean_{max}$ evenness was recorded in February (in the Elands control and Molenaars impact locations). An additional location effect for the Molenaars site was principally driven by naturally low, average evenness in early summer compared to other months (Appendix 7.6d). The location effect for the Du Toits was limited (Table 7.13) suggesting slight divergence between locations overall. Evenness values also were stable over the study period in the Riviersonderend R., both in time and between locations (Table 7.13 and Appendix 7.6d). In contrast with the other sites, lowest average evenness was experienced in midsummer at extremely low discharges (Feb: $\bar{x} = 0.414$).

Shifts in taxon evenness among biotopes at low flows

No significant differences in family-level evenness were found for biotopes under a natural low flow regime (one-way ANOVA: $F_{2, 213} = 1.352$, $P = 0.261$), as illustrated in Figure 7.14, though run assemblages showed higher average evenness. Negligible changes in evenness from overall values were observed when considering naturally lowest flows, so among-biotope differences remained non-significant (control: Figure 7.14). The consistent increases in assemblage evenness among biotopes observed at the Elands, from January to February, were not apparent at the other three sites, particularly under abnormally low flows (Appendix 7.7). With extreme discharge reduction, biotopes showed non-significant (Table 7.14), but detectable responses. Most apparent were lower mean ($\bar{x}_{impact} = 0.517$) and minimum riffle evenness than at natural low flows ($\bar{x}_{control} = 0.566$; Figure 7.14). For instance, in the Du Toits reach in February, the decline in riffle J' was coupled with markedly elevated evenness in runs ($\bar{x} = 0.814$ - site $mean_{max}$); the converse trend was apparent in the control location (Appendix 7.7). Additionally, the trend of increased evenness in pools at natural low flows was enhanced with further discharge reduction, when comparisons were made across biotope types; typically, lowest sample values were recorded for pool assemblages. Pool dominance decreased for flow-impacted locations in midsummer, when directly compared with pre-impact figures, for the Du Toits (Feb) and Riviersonderend (later, in Mar - to site $mean_{max}$). The opposite was true of the Molenaars location (similarly for riffles; see below and Appendix 7.7).

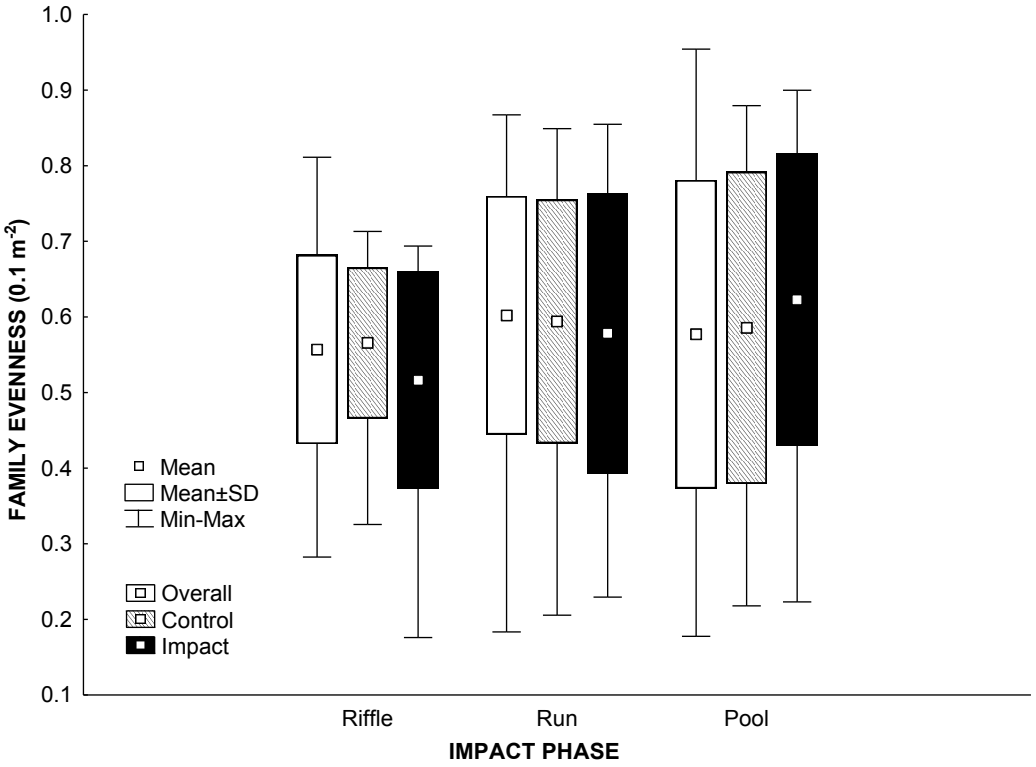


Figure 7.14 Statistical distribution of family-level evenness for invertebrate assemblages from different biotopes.

7.6.5 Assemblage diversity in relation to low flow regime and biotope type

Temporal and spatial patterns of diversity at family level

Patterns of family-level Shannon-Wiener diversity over the study period (depicted in Appendix 7.6e) showed a temporal variability in the Elands (ANOVA, month effect: $F_{5, 96} = 3.287$, $P = 0.009$) and especially Molenaars (ANOVA, month effect: $F_{5, 96} = 7.106$, $P << 0.001$) reaches that was lacking at the other sites. Tukey HSD results showed that, at both sites, the difference was largely a result of elevated diversity midsummer (especially Feb) relative to December (Appendix 7.6e). Shannon-Wiener diversity was spatially relatively consistent within each site reach, when locations were compared (Table 7.13). The absolute range in H' (as in the case of evenness) was recorded in the Du Toits reach, from 2.256 (pool, control location, Mar) to essentially zero where only one pool taxon was sampled (impact location, May).

Inter-biotope diversity at low flows

At natural low flows, in the Elands R., Shannon-Weiner diversity increased consistently across biotopes from January to the lowest flow period (Appendix 7.7). Under extreme low flows, the Molenaars River demonstrated no appreciable difference in overall or biotope-specific diversity from figures at natural discharges (Appendices 7.6e and 7.7), although pool diversity declined slightly. At the Du Toits site, from pre- to during-impact periods, biotopes in the impact location showed the opposite trend in diversity from that occurring under natural flows. In particular, riffle diversity was reduced to $\bar{x} = 0.627$ at extreme low

flows, while simultaneous observations in the control location showed mean values for this biotope of 1.538 (an increase from Jan). The diversity of run assemblages increased with extreme low flows to a February average of 2.076 (the site maximum average), in comparison with a decrease to $\bar{x}$ = 1.340 for the control location. Pool diversity in the Du Toits reach also increased from January to a higher level in the impact location than natural, reaching a maximum in March (Appendix 7.7). In contrast, pool diversity at the Riviersonderend site was markedly lower at extreme low flows, in February, than in the non-impacted part of the reach ($\bar{x}_{control}$ = 0.929 cf. $\bar{x}_{impact}$ = 0.513). The difference was no longer evident by March, when pool mean diversity markedly increased, along with diversity in runs. Diversity figures for the other two biotopes were also depressed at very low flows in February, when compared with figures for the unaffected reach section (Appendix 7.7). The overall trend in Shannon-Weiner diversity apparent for the site, based on the between-location response in this month, reflected this consistent pattern across biotopes ($\bar{x}_{min}$ = 0.855, in Feb impact location; Appendix 7.6e).

Although no significant inter-biotope differences in diversity were evident on the basis of control data over the total study period (one-way ANOVA: $F_{2, 213}$ = 2.944, P = 0.055), diversity was lower for pool assemblages than for runs or, particularly, riffles (Figure 7.15). In the peak of the dry season, although inter-biotope differences remained limited under natural flows, there were slight increases in mean faunal diversity for all biotopes (Elands site, Appendix 7.7, and control locations: Figure 7.15). At extreme low flows, there remained no significant inter-biotope differences in terms of average diversity, across the three impacted locations. Although riffle diversity declined ($\bar{x}_{control}$ = 1.397 cf. $\bar{x}_{impact}$ = 1.233), and with lower minima reached than at natural low flows during the impact phase (Figure 7.15), the change was insignificant (Table 7.14).

7.7 SPECIES RESPONSES TO LOW FLOWS: CHIRONOMIDAE AS A POTENTIAL INDICATOR FAMILY

Select classification and ordination analyses were conducted at comparable levels of resolution to the above analyses, to examine the extent to which chironomid species assemblages reflected family-level responses to low flow regimes. A summary of the species recorded from each site is provided in Appendix 7.8. A total of 45 species or species groups were recorded, of which only 19 were common to all sites. Orthocladiinae were dominant, representing 29 of the species total. Of the ten Chironominae, five each were in the Tanytarsini and Chironomini. Predatory tanypods totalled six species. Two new (Harrison 2000) and several unconfirmed species were found.

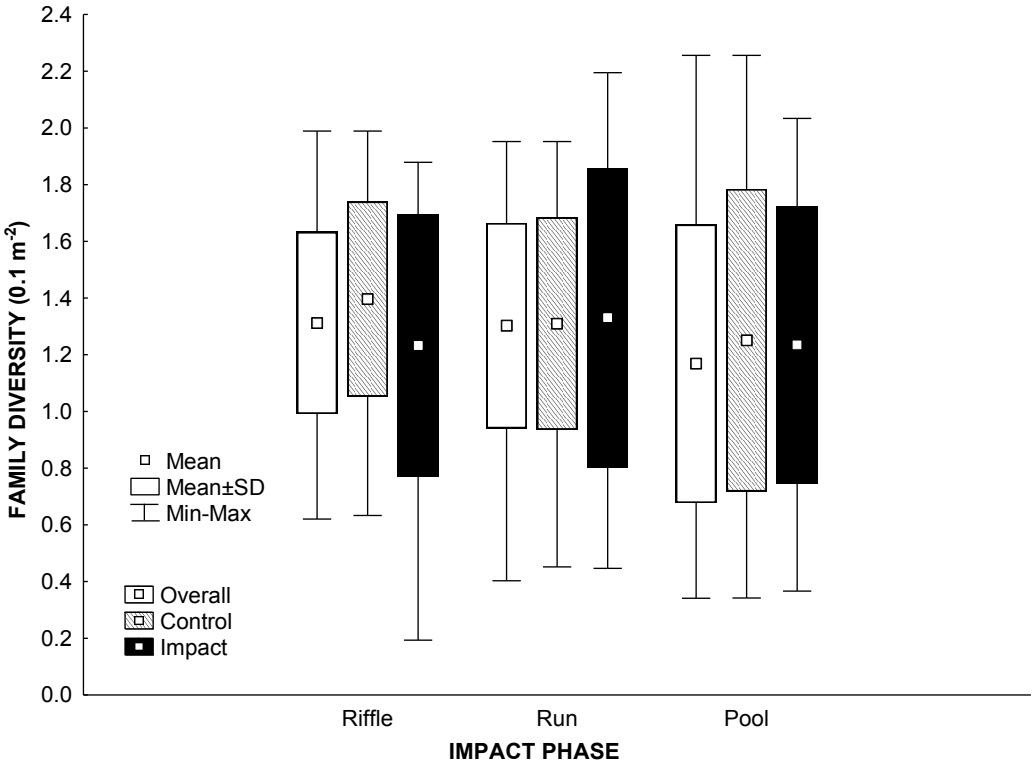


Figure 7.15 Statistical distribution of family-level Shannon-Wiener diversity for invertebrate assemblages from different biotopes.

7.7.1 Spatiotemporal changes in chironomid assemblages across sites at low flows

Given the limited overlap in chironomid composition from river to river (Appendix 7.8), as well as the distinct site specificity of invertebrate assemblages demonstrated at family level (Section 7.3.1), it is not surprising that site (river) signatures were largely retained when chironomid fauna from all sites were considered in combination (Figures 7.16a, b). The similarity between locations at each site, and the seasonal cohesiveness of the dry season, also remained apparent at species level (though a more limited range of months was considered than for family data). No obvious across- or within-site effects of extreme low flows were found. More evident than with family level analyses, however, was the distinctness of the chironomid fauna of the Riviersonderend River (at 53% Bray-Curtis similarity with the other sites). It exhibited the highest species richness (35 species cf. 24-30) and relative uniqueness (eight species not shared by any other site) of all sites (Appendix 7.8). In addition, within-site differences in chironomid composition over the study (especially in March cf. other months) were greater than those recorded among the other sites.

Analysis of similarities supported the limited overlap among sites, with highly significant differences for all site pairs (Table 7.15); results therefore were in accordance with those obtained at family level (cf. Table 7.1). The corresponding SIMPER analysis showed that within-site similarities in chironomid composition across the sites were similarly fairly high, ranging from 75% (Du Toits), through 74% (Molenaars) and 70% (Elands), to 66% at the Riviersonderend. The main species contributors to among-site dissimilarities are presented in Appendix 7.9.

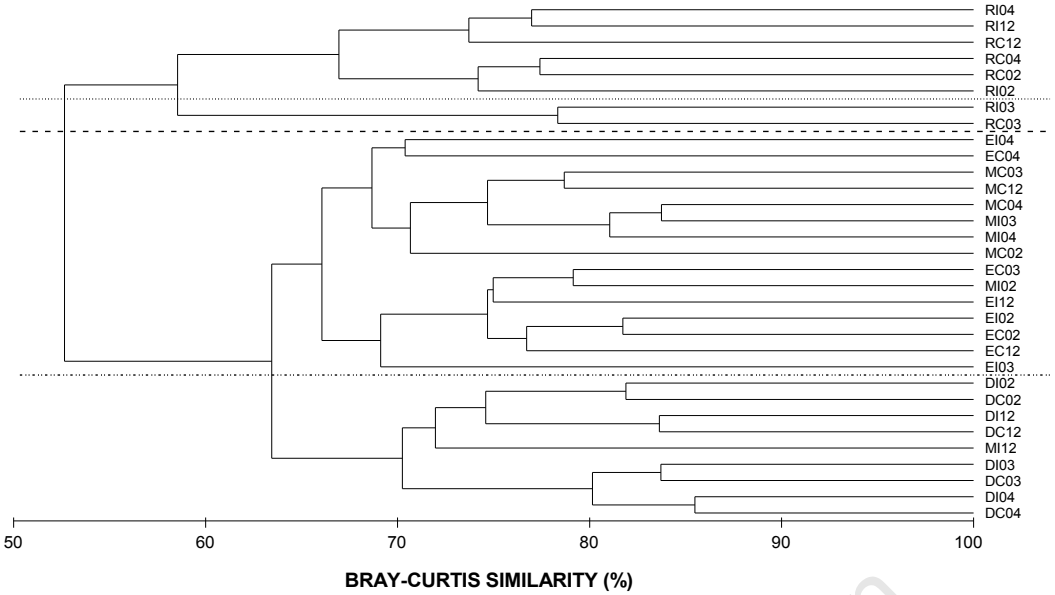


Figure 7.16 (a) Dendrogram of chironomid assemblages from site locations over the dry season (stone mean abundances 0.1 m^{-2}, all samples combined). E - Elands; M - Molenaars; D - Du Toits; R - Riviersonderend; C - control location; I - impact location; 12-04 indicates month, from Dec-Apr. Major group divisions are delineated.

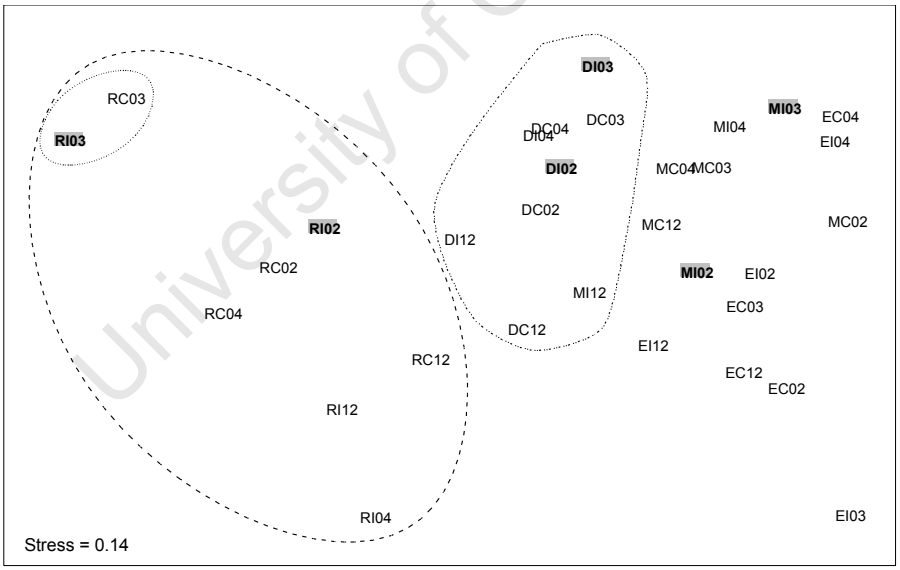


Figure 7.16 (b) Ordination plot based on the same similarity matrix as Figure 7.16a. The three main clusters from the dendrogram are superimposed. Chironomid assemblages subjected to extreme low flows are in bold and shaded.

As at family level, the lowest dissimilarity in chironomid composition was observed for the Molenaars and Elands rivers, with the overriding difference attributable to elevated abundances in the former reach of several shared species (Appendix 7.9). These species included three chironomids that attained maximum

abundances overall in the Molenaars River, *Thienemanniella trivittata* (72.4 individuals 0.1 m^{-2}), *Nilotanypus comatus* (4.9 individuals 0.1 m^{-2}), and *Rheotanytarsus fuscus* (43.4 individuals 0.1 m^{-2}). The Riviersonderend and Elands rivers diverged most of all site pairs (Table 7.15 and Appendix 7.6). Notably, the Riviersonderend reach was characterised by *Parakiefferiella biloba* (and other *Parakiefferiella* spp. - Appendix 7.8), which was absent from the other sites. The Riviersonderend also exhibited the highest abundances of *Polypedilum* spp. (32.5 0.1 m^{-2}) across sites. The Du Toits River shared several species with the Riviersonderend that were absent or in low numbers at the other two sites (Appendix 7.9), including Orthoclad sp. A (a marker species for the Riviersonderend R.), *Stempellina truncata*, and *Cricotopus* sp. L. The Du Toits reach was further differentiated from the other sites in possessing the highest densities (137.0 0.1 m^{-2}) of the small, common orthoclad, *Notocladius capicola*.

Table 7.15 One-way ANOSIM results for among-site comparisons of chironomid assemblages (species mean abundances 0.1 m^{-2}). R statistics for pairwise tests are followed by *P* values in parentheses (highly significant: $P \leq 0.001$).

FACTOR		PAIRWISE TESTS FOR GROUPS				
Site			Elands	Molenaars	Du Toits	Riviersonderend
Global R	0.716	Elands		0.478 (0.001)	0.821 (0.001)	0.896 (0.001)
P	0.001	Molenaars			0.744 (0.001)	0.887 (0.001)
		Du Toits				0.747 (0.001)
		Riviersonderend				

7.7.2 Dynamics of chironomid-biotope associations in relation to low flow regimes at individual sites

On the basis of the site-specificity of chironomid assemblages, as well as the results obtained for family-level analyses of individual sites with biotopes pooled (see Section 7.3), the degree of association of chironomid species with different biotopes under low flow conditions was examined separately for each site (Table 7.16). Consideration was given to location and seasonal effects.

Classification and ordination analyses for the natural low flow regime, at the Elands site (Figure 7.17), were supported by ANOSIMs which indicated no effect of location (Global R = -0.064, *P* = 0.935) or season (Global R = -0.003, *P* = 0.462; Table 7.16) on chironomid assemblages (as also the case at family level). Analyses of similarity comparing the two locations at the site independently for the months of February and March also showed no significant inter-location effects (similarly absent for the other sites – not discussed further here). In contrast, as shown for whole invertebrate assemblages, there was a distinct and highly significant association of chironomid species with biotope type (Global R = 0.503, *P* = 0.001; Table 7.16).

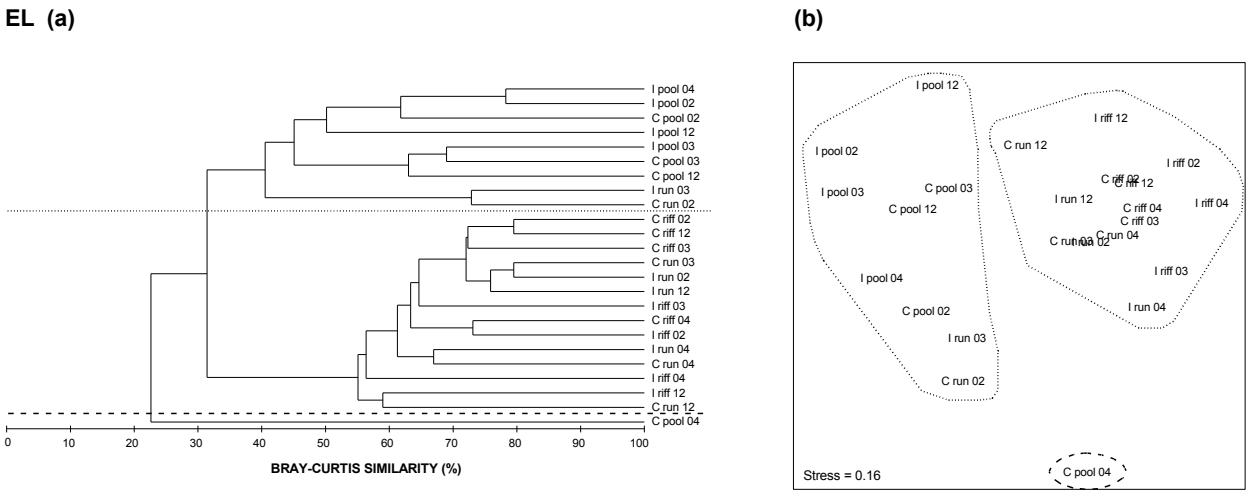


Figure 7.17 (a) Dendrogram of chironomid assemblages from riffle, run and pool biotopes at the Elands site over the dry season (stone mean abundances 0.1 m^{-2}). C - control location; I - impact location; 12-04 indicates the month, from Dec-Apr. Primary (dashed line) and secondary (dotted line) group divisions are indicated. **(b) Ordination plot based on the same similarity matrix as Figure 7.17a.**

Chironomid assemblages appeared to show stronger association with either pools or runs, in particular, than apparent when considering family-level data (Figure 7.17 cf. Figure 7.2; Table 7.16 cf. Table 7.6). Tanypod *Paramerina* spp. were the main group of chironomids that attained higher densities in pools than runs (2.5 vs. 0.1 individuals 0.1 m^{-2}, respectively; see Appendix 7.10 for full SIMPER results). At the peak of the dry season, there was a tendency for run assemblages to cluster with those of pools. Though not without species overlap (R = 0.235), the composition of riffle and run assemblages at the control site remained significantly different at P = 0.001 (48% dissimilarity). The difference was mostly attributable to larger numbers of shared species inhabiting riffle patches, including *Notocladius capicola* (mean of 47.0 individuals 0.1 m^{-2}), *Rheotanytarsus fuscus* (12.1 0.1 m^{-2}), and *Thienemanniella trivittata*. Elevated abundances of these species, as well as of *T. lineola, Polypedilum* and *Cricotopus*, were primarily responsible for the marked difference in composition also found between riffles and pools. Several species, notably *R. fuscus* (at $\overline{\delta}_i$ / SD (δ_i) ratio = 3.23, the best biotope discriminator of all), *T. trivittata* and *T. lineola* appeared to be suitable indicators of different biotope types.

The Molenaars site showed no significant between-location difference in overall chironomid composition (Figure 7.18 and Table 7.16). Similarly, no significant fluctuations in species composition in relation to season were observed (Table 7.16), consistent with the stable low flow regime at this site (also the case for the Elands R.; Chapter 4). The clear association of different assemblages of chironomids with riffles, runs and pools (Global R = 0.415, P = 0.001), also observed for invertebrate families (Figure 7.3), was pronounced for riffles and runs, as compared with pools (Figure 7.18 and Table 7.16).

Table 7.16 One-way ANOSIM results for comparisons of chironomid species assemblages from different locations, biotopes and months, for individual sites. R statistics are followed by *P* values in parentheses, with significant results ($P \leq 0.050$) in bold italics. Samples represented mean abundances 0.1 m^{-2}. E - Elands; M- Molenaars; D - Du Toits; R - Riviersonderend.

FACTOR	GLOBAL R (*P*)		PAIRWISE TESTS FOR GROUPS R (*P*)			
Location	E -0.064 (0.935) M -0.037 (0.872) D -0.020 (0.605) R -0.037 (0.697)					
			Riffle	Run	Pool	
Biotope	***E 0.503 (0.001)*** ***M 0.415 (0.001)*** ***D 0.447 (0.001)*** ***R 0.265 (0.004)***	Riffle				
		Run	***E 0.235 (0.001)*** ***M 0.196 (0.006)*** ***D 0.267 (0.016)*** R 0.170 (0.085)			
		Pool	***E 0.797 (0.001)*** ***M 0.609 (0.001)*** ***D 0.719 (0.001)*** ***R 0.402 (0.007)***	***E 0.424 (0.005)*** ***M 0.501 (0.001)*** ***D 0.417 (0.002)*** ***R 0.218 (0.036)***		
			Dec	Feb	Mar	Apr
Month	E -0.003 (0.462) M 0.002 (0.422) ***D 0.152 (0.024)*** ***R 0.340 (0.002)***	Dec				
		Feb	E -0.019. (0.502) M -0.035 (0.628) D 0.191 (0.056) ***R 0.237 (0.032)***			
		Mar	E -0.033 (0.537) M 0.002 (0.429) ***D 0.344 (0.006)*** ***R 0.965 (0.002)***	E -0.106 (0.801) M 0.011 (0.366) D 0.080 (0.180) ***R 0.309 (0.050)***		
		Apr	E 0.126 (0.091) M 0.087 (0.136) ***D 0.383 (0.015)*** R 0.031 (0.310)	E -0.026 (0.481) M 0.020 (0.297) D 0.020 (0.340) R 0.102 (0.171)	E 0.057 (0.245) M -0.048 (0.708) D -0.020 (0.504) ***R 0.463 (0.011)***	

The Molenaars SIMPER results (Appendix 7.11) indicated that the main divergence between riffles and pools was attributable to comparatively very low abundances of *Rheotanytarsus fuscus* (< 0.1 animal 0.1 m^{-2}) and *Notocladius capicola* (1.0 individuals 0.1 m^{-2}), coupled with an absence of *Rheocricotopus capensis*, in pools; the first two species showed potential as biotope discriminators. Delimitation of pool and run assemblages was founded on lower numbers of five species in the former biotope, as well as an absence of *Tvetenia calvescens* (mean abundance = 3.5 0.1 m^{-2}, in runs), a potential indicator species (Appendix 7.11). At family level, the run assemblage reflecting flow reduction in February (sample 'I run 02' - Figure 7.3a) clustered with pool assemblages, a pattern that was no longer evident at species level (control and impact samples grouped, though at a fairly low percentage similarity). Lowest separation by biotope was apparent for assemblages of riffle- and run-dwelling chironomids (Figure 7.18; R = 0.196, *P* = 0.006, Table 7.16), mainly due to their possessing several common species (Appendix 7.11). Although chironomid densities were generally lower in runs than riffles, *Thienemanniella trivittata* and *Polypedilum* spp. exhibited elevated numbers (the converse was true at the Elands site for the first species). *Polypedilum* spp. was highlighted as a potential discriminatory group for the two biotopes.

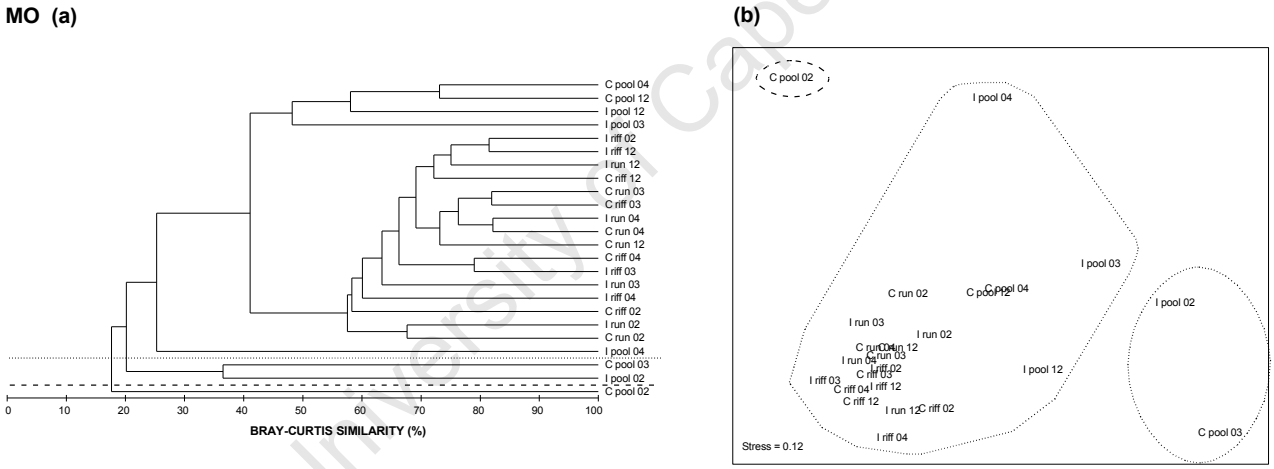


Figure 7.18 (a) Dendrogram of chironomid assemblages from riffle, run and pool biotopes at the Molenaars site over the dry season (stone mean abundances 0.1 m^{-2}). C - control location; I - impact location; 12-04 indicates the month, from Dec-Apr. Primary (dashed line) and secondary (dotted line) group divisions are indicated. **(b) Ordination plot based on the same similarity matrix as Figure 7.18a.**

At the Du Toits site, classification and ordination results (Figures 7.19a, b, respectively), were also in agreement with those of one-way ANOSIMs (Table 7.16). Although there remained no influence of location on chironomid assemblages at species level, there was evidence of a significant seasonal (and hence, hydrological) effect from December to April (Global R = 0.152, *P* = 0.024; pairwise test results for all months are presented in Table 7.16). In particular, December chironomid assemblages tended to cluster apart from those of other months; the influence was less strong than that of biotope.

Biotope-species associations in the Du Toits reach were highly significant (P = 0.001), with a corresponding Global R value of 0.447. The main divisions on the basis of Bray-Curtis similarities separated pool-dwelling chironomid fauna, the most variable biotope assemblage, from most other samples (Figure 7.19). Pools were characterized by elevated densities of *Paramerina* spp. (6.1 individuals 0.1 m^{-2}, vs. riffles: 1.1 and runs: 1.3) and juvenile tanypods (6.7 individuals 0.1 m^{-2}), with the latter absent from the other two biotopes (Appendix 7.12). Additionally, numbers of many species common to riffles and runs, including *Cricotopus* and *Tanytarsus* species were lower in pools. Of these chironomids, *Notocladius capicola* and *Rheocricotopus capensis* emerged as candidate discriminatory species. Except for early summer (December), pool and run species-assemblages were distinct (and more so than at family level - cf. Figure 7.4; R = 0.417, P = 0.002). Although the flow-impacted pool assemblage from March separated from all other pool samples, there were similarly high ordination distances for control assemblages (Figure 7.19b), suggesting no detectable impact of extremely low discharges on pool fauna (see also Section 7.7.3). There was a greater mix of riffle and run assemblages than evident at higher taxonomic levels (Figure 7.19 cf. Figure 7.4), supported by the weakest ANOSIM result for this biotope pair (R = 0.267, P = 0.016; Table 7.16). Corresponding SIMPER results showed that Du Toits riffles tended to exhibit greater abundances of species shared with runs (notably for *Notocladius capicola*, with 361.0 riffle individuals 0.1 m^{-2}), except for *Thienemanniella trivittata* (Appendix 7.12). Possible discriminatory species were *Rheocricotopus capensis* (22.8 and 2.1 individuals 0.1 m^{-2} in riffles and runs, respectively) and, to a lesser extent, *Stempellina truncata.* Although the flow-impacted chironomid assemblages of runs were more similar in composition, on average, to those of control riffles in February (see also the separation of Feb run samples from the main cluster of run samples at family level in Figure 7.4), the naturally high degree of overlap evident between fauna of the two biotopes rendered the result inconclusive (see also Section 7.7.3).

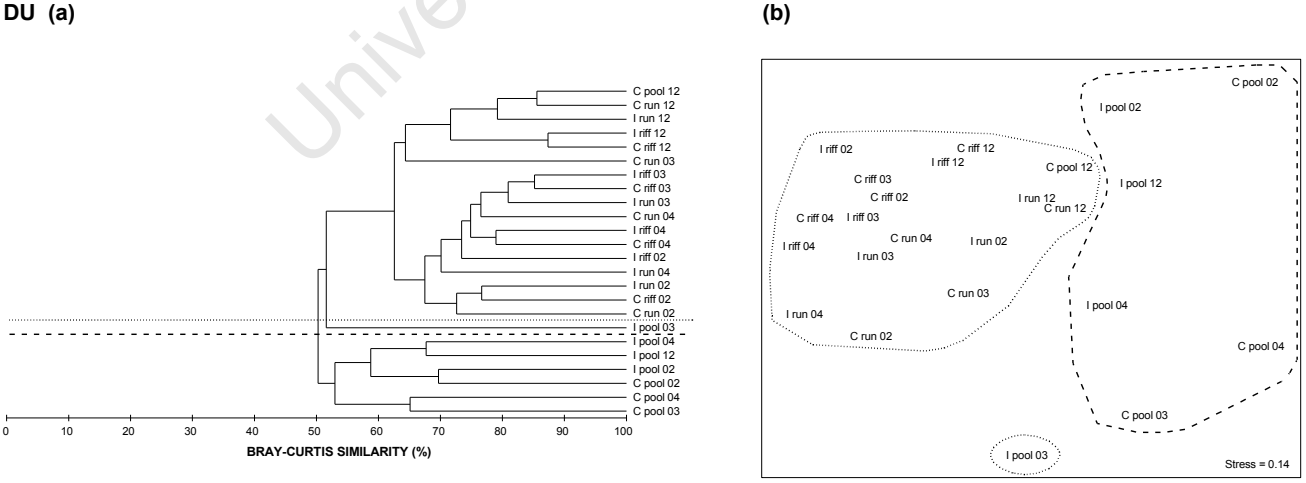


Figure 7.19 (a) Dendrogram of chironomid assemblages from riffle, run and pool biotopes at the Du Toits site over the dry season (stone mean abundances 0.1 m^{-2}). C - control location; I - impact location; 12-04 indicates the month, from Dec-Apr. Primary (dashed line) and secondary (dotted line) group divisions are indicated. **(b) Ordination plot based on the same similarity matrix as Figure 7.19a.**

Consistent with family-level analysis, as well as the results for other sites, there was no significant difference between the Chironomidae of control and impact locations in the Riviersonderend reach (Table 7.16 and Figure 7.20), irrespective of experimental discharge reduction. In contrast, the significant seasonal variation in species composition (Global R = 0.340, $P = 0.002$) was more pronounced at this site than in the Du Toits reach. Pairwise tests showed that there were detectable differences among assemblages marking the onset and end of summer, as well as within the peak period of low flows (Table 7.16). The December chironomid fauna tended to group apart from those of the other months examined, with pool assemblages seeming allied with those of runs in early summer.

Inter-biotope differentiation was weakest of all sites at the Riviersonderend, but still significant (Global R = 0.265, $P = 0.004$), generally the same trend as found at family level (Table 7.6). Notably, the composition of riffles and runs was not detectably different on the basis of their Chironomidae (R = 0.170, $P = 0.085$; Table 7.16). Apart from an absence of *Conchapelopia trifascia* in runs, a species with high discriminatory potential, the two biotopes differed primarily in the densities of shared larvae (Appendix 7.13 provides SIMPER results). Runs possessed higher numbers than riffles of *Parakiefferiella biloba*, *Thienemanniella sp. R*, *T. lineola* and *Cricotopus sp. L*. In riffles, the dominant chironomid was *Notocladius capicola* (95.2 individuals 0.1 m^{-2} vs. only 10.3 0.1 m^{-2} in runs, and 1.3 0.1 m^{-2} in pools). In March specifically, when discharges were low, assemblages of riffles and runs showed higher degrees of similarity with those of pools than at other times (Figure 7.20). In that period, there was a tendency for chironomids of flow-impacted riffles to resemble those of control runs, and the converse. Given the high natural invertebrate overlap of these two biotopes, however, it cannot be stated with certainty that there was any impact of abnormal discharges (a conclusion also reached in Section 7.7.3). Chironomid assemblages associated with pools and runs were significantly different, with *Polypedilum* spp. a useful discriminator, reaching average densities (0.1 m^{-2}) of 79.4 (the dominant species) and 3.9, respectively. Abundances of *Ablabesmyia dusoleili* and *Nanocladius spp.* were also markedly elevated in pools as compared with runs (Appendix 7.13). As at family level, chironomids inhabiting previously flow-impacted pools, in April, split from all other assemblages at only 33% similarity (Figure 7.20a; ANOSIM result: Global R = 0.883, $P = 0.042$). A SIMPER analysis, focused on contributors ≤ 50% similarity, indicated that the sample shared only one species out of seven with the other cluster, namely *Corynoneura cristata*.

7.7.3 Responses of chironomids associated with different biotopes to extreme low flows

Given the outcomes of family-level analysis during the impact phase (Section 7.4.3), analysis of any direct changes in species assemblages midsummer, with the shift from natural to artificially reduced discharges, focused on between-location differences by biotope, for individual rivers. The ANOSIM results are presented in Table 7.17 (impact data combined). Classification and ordination, which supported the ANOSIM results, yielded similarly subtle shifts in assemblages to those occurring at family level, suggesting a direct but localised influence of hydraulics; therefore, individual plots are not presented.

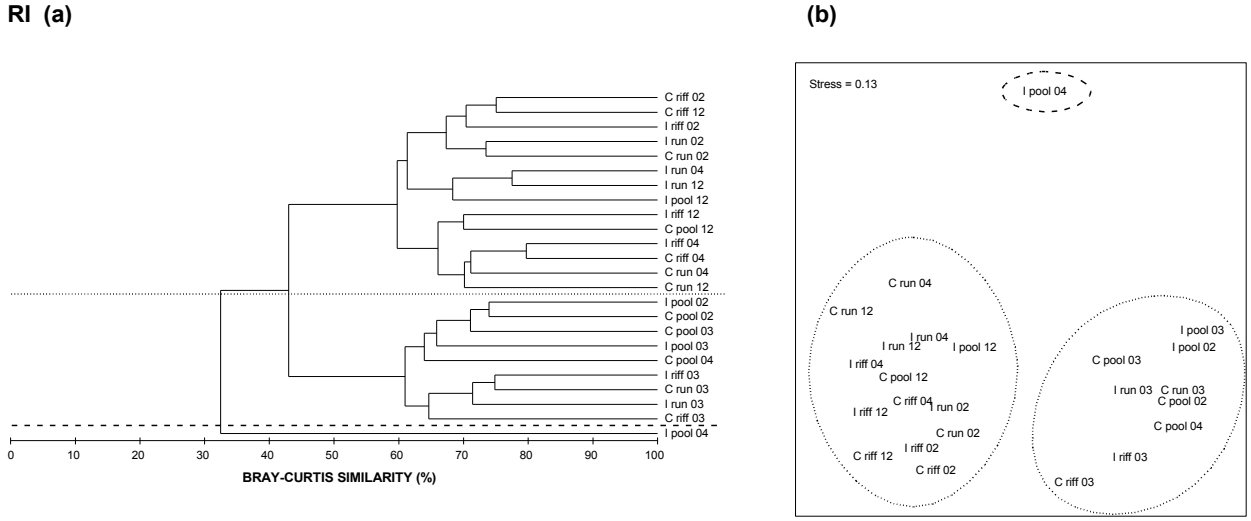


Figure 7.20 (a) Dendrogram of chironomid assemblages from riffle, run and pool biotopes at the Riviersonderend site over the dry season (stone mean abundances 0.1 m^{-2}). C - control location; I - impact location; 12-04 indicates the month, from Dec-Apr. Primary (dashed line) and secondary (dotted line) group divisions are indicated. **(b) Ordination plot based on the same similarity matrix as Figure 7.20a.**

While under natural flow conditions (Elands) the biotope specificity of midge assemblages was amplified mid-dry season (as compared with findings at family level), assemblages at the experimental sites showed slightly reduced differences in species composition among the major hydraulic biotopes, based on comparisons of Global R values (Table 7.17 cf. family-level results of Table 7.8).

Analyses using chironomid species gave similar results to that of invertebrate families at the Elands site, with within-biotope consistency across the reach (R values: riffles = 0.050; runs = 0.015; pools = -0.032). A greater divergence of run assemblages from those of both riffles and pools was apparent at species level, though not consistent between locations. When February and March data were analysed independently for the control and impact locations, runs remained the most variable biotope in species composition. In February, riffles remained most similar within the reach while pools showed the highest internal similarity in assemblage composition in March (two pool samples without chironomids were omitted from analyses).

At the Molenaars site, although there was no statistically significant effect of extremely reduced discharge within any biotope, there was an overall decline in assemblage biotope specificity at species level (Table 7.17 cf. Table 7.8). In particular, riffles and runs showed increased similarity in chironomid composition. Runs were most similar internally in both instances when the impact phase data were disaggregated by month. In February and March, ANOSIM pairwise R values for the control and impact locations for the main biotopes indicated least similarity among pools and riffles, respectively. Results were limited by the required omission of three samples (all from pools) lacking chironomids.

Table 7.17 One-way ANOSIM results for individual sites, comparing chironomid species assemblages from different biotopes within the control and impact locations during the impact phase (February-March). R statistics for pairwise tests are followed by *P* values in parentheses (* - significant).

FACTOR SITE	LOCATION BIOTOPE Global R	*P*			PAIRWISE TESTS FOR GROUPS					
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Elands (control)	0.433	*0.001	Control	Riffle						
				Run	0.409 *(0.006)					
				Pool	0.872 *(0.002)	0.239 *(0.048)				
			Impact	Riffle	0.050 (0.227)	0.302 *(0.017)	0.798 *(0.002)			
				Run	0.454 *(0.009)	0.015 (0.381)	0.061 (0.307)	0.469 *(0.006)		
				Pool	1.000 *(0.005)	0.817 *(0.005)	-0.032 (0.543)	0.923 *(0.005)	0.369 *(0.033)	
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Molenaars	0.338	*0.001	Control	Riffle						
				Run	0.128 (0.115)					
				Pool	0.600 *(0.002)	0.507 *(0.002)				
			Impact	Riffle	0.206 (0.067)	0.059 (0.219)	0.640 *(0.002)			
				Run	0.285 *(0.022)	0.043 (0.305)	0.368 *(0.019)	0.209 (0.056)		
				Pool	0.671 *(0.005)	0.480 *(0.010)	0.106 (0.246)	0.677 *(0.005)	0.258 (0.071)	
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Du Toits	0.289	*0.001	Control	Riffle						
				Run	0.419 *(0.022)					
				Pool	0.535 *(0.002)	0.328 *(0.019)				
			Impact	Riffle	0.163 (0.097)	0.429 *(0.006)	0.544 *(0.002)			
				Run	0.467 *(0.004)	-0.061 (0.658)	0.348 *(0.002)	0.387 *(0.011)		
				Pool	0.283 *(0.002)	0.085 (0.214)	-0.138 (0.844)	0.320 *(0.002)	0.228 *(0.015)	
					Control			Impact		
					Riffle	Run	Pool	Riffle	Run	Pool
Riviersonderend	0.249	*0.001	Control	Riffle						
				Run	0.226 (0.061)					
				Pool	0.769 *(0.002)	0.322 *(0.006)				
			Impact	Riffle	0.009 (0.394)	-0.024 (0.476)	0.409 *(0.002)			
				Run	0.343 *(0.022)	-0.020 (0.504)	0.243 *(0.032)	0.061 (0.201)		
				Pool	0.715 *(0.002)	0.263 *(0.030)	0.015 (0.364)	0.454 *(0.002)	0.289 *(0.009)	

At the Du Toits site, in midsummer, extreme low flows resulted in no significant within-biotope responses in chironomid assemblages between locations (Table 7.17), mirroring family-level results (Table 7.8). Although there was a tendency for assemblages of impacted pools to resemble those of un-impacted runs (R = 0.085, *P* = 0.214), the converse was not true (R = 0.348, *P* = 0.002). Family level flow-impacted run and pool faunas were similar during the impact phase, but assemblages diverged significantly (R = 0.228 *P* = 0.015) at species level. When February data for the two locations was examined independently, pairwise R values showed the lowest similarity was for runs and the highest for pools. In March, all three biotopes had very similar R values, with pools again showing the highest within-reach similarity. Results for this site likely were influenced by limited sample replication, with three pool and one run sample without any chironomids.

The Riviersonderend was the sole site at which chironomids were present in all midsummer samples. Results for flow-impacted riffles and runs (Table 7.17) entirely matched those at family level (Table 7.8) in showing no detectable response of chironomids to extreme low flows. The same pattern held for pools at species level, although there was a significant difference between natural and low-flow pool assemblages when data were analysed on the basis of families (see above). Differences between run and pool assemblages were greater at extremely reduced discharges, at species level (R = 0.289, *P* = 0.009) when compared with family results, as also recorded in the Du Toits impact location. When February and March data for hydraulic biotopes were compared independently between locations, all biotopes exhibited very similar R values, particularly in February. Pools and riffles showed the greatest and lowest within-reach similarity for both months (pairwise R values from ANOSIM analysis), respectively.

7.8 SUMMARY AND DISCUSSION

Direct responses of benthic macroinvertebrate assemblages to short-term changes in low flow regime, that included discharge reductions (36-86%) to below historical minima and for extended durations of nearly two months, were fewer, subtler and less consistent than disturbance effects on instream physical habitat. This was by no means atypical, with relatively mild or inconsistent invertebrate responses to various low-flow disturbances, even severe artificial flow reductions, reported for other perennial rivers (e.g. Iversen *et al.* 1978; Ladle and Bass 1981; Canton *et al.* 1984; Chessman and Robinson 1987; Cuffney and Wallace 1989; McElravy *et al.* 1989; Dudgeon 1992b; Bickerton 1995; Castella *et al*. 1995; Armitage and Pardo 1995; Englund and Malmqvist 1996; Rader and Belish 1999; Wood *et al.* 1999; Choy *et al.* 2000; Caruso 2002; Suren *et al.* 2003; Dewson *et al*. 2003, 2007a, b, McIntosh *et al*. 2008). In certain instances, more distinct changes in assemblages with low flows have been detected, particularly for specific taxon groups or biotic response measures, often within these same studies or those of a similar nature (e.g. Hynes 1958; Larimore *et al.* 1959; Ward 1976; Gore 1977; Extence 1981; Cowx *et al.* 1984; Wright and Berrie 1987; Delucchi 1988; Hooper and Ottey 1988; Armitage and Petts 1992; Wood and Petts 1994, 1999; Pollard *et al.* 1996; O'Keeffe

and Uys 1998; Cazaubon and Giudicelli 1999; Davies *et al*. 2000; Ledger and Hildrew 2001; McIntosh *et al*. 2002).

Considerable variation in riffle invertebrate responses occurred with unnatural flow reductions ranging from 28 to 98% below abstraction points on four lowland New Zealand streams, but was largely attributed to natural among-stream differences in assemblage composition and physicochemistry (Dewson *et al*. 2003) that were far less pronounced among the rivers in the present study (Chapter 2). Limited and sometimes inconsistent differences in benthic composition were detected with diversion of 98% of summer daily baseflow in the perennial, but naturally flow variable, upper Waihee River, Hawaii (McIntosh *et al*. 2008). In contrast, in another smaller, flow-variable perennial Hawaiian stream, marked shifts in riffle composition occurred with similar magnitude flow diversion (McIntosh *et al*. 2002). Experimental discharge reduction of 89 to 98%, for one dry-season month, had variable effects on assemblage structure in three New Zealand streams (Dewson *et al*. 2007a, b; Death *et al.* 2009). As in the current study, there was no simple graded invertebrate assemblage response to flow magnitude, but the near-pristine stream showed the greatest and the most anthropogenically altered stream the least response to the disturbance. Conversely, in three perennial U.S. mountain streams, the degree of direct response by riffle fauna was closely dependent on whether flow diversion was mild or severe (Rader and Belish 1999); streams could not be compared, because of distinct differences in biophysical character. Across sites on 22 different U.K. streams subjected to diverse kinds of water abstraction, the relationship between annual abstraction intensity and extent of invertebrate response was limited, with regional factors more influential than any localised effects (which were insignificant). Although minor discharge reductions typically lead to lower levels of change in assemblages than moderate to major disturbances, there remained a lack of coherence in response with "a multiplicity of possible trends in faunal response to reduced flow conditions" (Castella *et al*. 1995, p. 181). While focused assessment for rivers of the same biophysical type was more effective in characterizing invertebrate response, trends remained limited and inconsistent at family and species levels. Even in the current study, despite comparatively similar invertebrate composition, hydrology and other biophysical conditions (Chapter 2), the four rivers studied needed to be addressed separately in terms of many reactions to low-flow disturbance.

The limited evidence in the current study of direct responses to low flows at the scale of multiple rivers and reaches, as well as at different taxonomic levels, firmly established the importance of focusing attention at fine levels of the geomorphologic hierarchy within individual reaches, to discern any biotic response with confidence (Armitage 1995; Pardo and Armitage 1997); this despite the difficulty of identifying more regular (predictable) statistical behaviour for smaller temporal windows and spatial patches (Levin 1992; Downes *et al*. 1993). Without doubt, however, the adoption of multiple spatiotemporal scales proved invaluable in consolidating understanding of invertebrate responses to flow (Minshall 1988; Ward 1989; Boulton and Lake 1992a; Robson 1999). Particularly, some gains in the generality and consistency of responses were achieved by moving to progressively broader scales of assessment, as more variation was introduced with changes in study extent and grain (Wiens 1989; Kotliar and Wiens 1990; Boulton and Lake 1992a).

Not unexpectedly (Resh *et al*. 1988; Yount and Niemi 1990) and also apparent from other low flow studies (Minshall and Petersen 1985; Morrison 1990; Boulton and Lake 1992a; Dudgeon 1992b), direct responses to disturbance were difficult to disentangle from patterns of natural variability in biotic diversity and composition within and across rivers. As Dunbar and Acreman (2001, p. 9) observed, in ecohydrological studies "Observation of cause and effect is unfortunately often confounded by the extensive natural variability that river systems exhibit". This was arguably more the case here, where the physical disturbances represented the exacerbated effects of low flow as a natural stressor (Section 1.4.4), and where invertebrate response might simply have been an extension of characteristic responses to low flow variation usually experienced in these rivers (Boulton 2003). The focus on a discrete disturbance event and for least-altered upper rivers did help avoid potentially confounding effects of multiple cumulative or press disturbances (Bender *et al.* 1984; Lake 2000), more commonly encountered in middle to lower reaches, on the detection of disturbance (Niemi *et al*. 1990). Caution still had to be exercised in making inferences regarding causal relations between flow and invertebrate response, as it would also have to be in wider extrapolation of the results of this experimental study (Fisher 1987; Fisher and Grimm 1988; Minshall 1988; Brooks and Boulton 1991), due to its small scale, short duration, and limited replication of flow impact (Townsend 1989; Doeg *et al*. 1989; Richter *et al*. 1997a; Matthaei *et al*. 1997).

Such considerations aside, there was evidence of strong influences of both the catchment affiliations of site assemblages (Wishart 2000) and within-catchment individual 'river signatures', as recognised by other researchers (Ward 1976; Armitage and Petts 1992; Scarsbrook and Townsend 1993; Castella *et al.* 1995; Kay *et al.* 1999; Petts *et al*. 1999; King and Schael 2001; Suren *et al*. 2003; McIntosh *et al*. 2008; Konrad *et al*. 2008). These dominated over influences of season and hence, month or broad flow state, as well as within-reach geomorphological character. Although this result, also encountered when seeking generic responses to the effects of low flows on chemistry and physical habitat (Chapters 5 and 6), limited the utility of an independent control river, as its invertebrate assemblages might have been responding to low flow signals in ways inconsistent with those of other sites, it accentuated the invaluable role of control locations at individual experimental sites (rivers) in distilling out atypical from natural biotic responses (Section 2.3). As individual rivers often showed site-specific responses to low flows, and fine relationships with flow tended to be obscured with all rivers addressed in aggregate, the majority of analyses had to be run independently by site, rendering it more difficult to detect certain types of responses with the reduction in statistical power.

7.8.1 General effects of natural and artificial low flows on invertebrate assemblages of multiple rivers

Overall changes in spatiotemporal composition of assemblages with low flows

An appreciable seasonal assemblage response to natural flow regimes was lacking, suggesting that any defining wet-season high flow events had yet to occur. Also, even at this scale, the strong influence of the hydraulic biotope character of these upper rivers tended to override other influences on the benthos, with few

distinct trends in assemblage composition due to dry-season flow pattern. Seasonal dynamics were also secondary to spatial variation in influencing invertebrate composition of mesohabitats in Mill Stream, U.K. (Armitage *et al*. 1995; Pardo and Armitage 1997). In contrast, in the upper Buffalo River, South Africa, the effects of season on assemblage structure were more pronounced than the influence of biotope type (Palmer *et al.* 1991). In the current study, the stability of assemblages (*sensu* Death and Winterbourn 1994; Death 1996a, b) matched that evident in natural hydrological regimes over the dry season, however, and particularly midsummer (Section 4.5.1). A few shifts in composition were concomitant with natural discharge declines and increases that, in part, were early signals of the onset of the dry season and autumn, respectively. The only wholly consistent trend across rivers though was a decline in densities of Baetidae, a known flow sensitive family (Larimore *et al*. 1959; Ward 1976; Ward and Short 1978; Lillehammer and Saltveit 1984b; Saltveit *et al*. 1987; Brittain and Saltveit 1989; Castella *et al*. 1995; Rader and Belish 1999; O'Keeffe and Dickens 2000; Wood *et al.* 2000), to lowest levels overall with higher flows at the very end of the dry season. As Brittain and Saltveit (1989, p. 199) observed "when the discharge regime is altered the mayfly community will change". Lower numbers of hydropsychids and leptocerids also occurred in the latter part of the dry season in certain rivers, while hydroptilids and teloganodids conversely increased with elevated flows early autumn. Simuliidae, in contrast, exhibited both directions of response to natural low flow regimes, with highest or lowest abundances in early autumn. Most of these families are also well recognised as including flow responsive species (Larimore *et al*. 1959; Ward and Stanford 1979; Hauer *et al*. 1989; Brittain and Saltveit 1989; O'Keeffe and Dickens 2000; Wood *et al.* 2000; Growns and Growns 2001). Interestingly, for the river for which the low flow regime was most variable and least predictable in terms of its natural disturbance history, and from which most flow was experimentally diverted, changes in invertebrate assemblage and species (Chironomidae) composition mirrored the flow fluctuations at a monthly temporal window (see also Sections 8.7 and 8.8).

No statistically significant changes in overall assemblage composition (collectively across all types of streambed patches) commensurate with the intensity of artificial low-flow disturbance were apparent. Species-level results accorded entirely with those at family level, irrespective of fewer than half the chironomid species being common to all rivers and a highly distinct chironomid fauna in the most flow-reduced reach. This match in response minimised the possibility that reliance in higher taxonomic levels might lead to an underestimation of flow effects, as posited by Growns and Growns (2001). Slight divergence in the composition of flow-impacted assemblages from those experiencing natural low flows, immediately after artificial flow reduction was initiated and for all biotopes in one river, did provide a first indication of a disturbance effect once flows fell below historical minima. In the other highly flow disturbed, but naturally flow variable river, there was evidence of limited and lagged (several weeks) assemblage divergence with time since flow disturbance, a phenomenon also reported by Feminella and Resh (1990) and Boulton and Lake (1992a, b). There was no obvious overall assemblage response for the river at which the least discharge was diverted. In both highly flow-altered rivers, assemblages seemed not only resistant, but also highly resilient (Section 1.4.3), showing the rapid recovery common with low-flow disturbances

(Section 7.1.6) and a stable assemblage structure by autumn. For three N.Z. streams, experimental flow diversion of on average 89% to 94% (but at times exceeding 97%) in summer similarly led to varying degrees of divergence in the composition of riffle assemblages between locations experiencing natural and extreme low flows (Dewson *et al*. 2007a); natural assemblage structure differed for each stream. In two of the streams, the communities became increasingly dissimilar over time to the extent that the natural-flow and impact communities were distinctly different in composition after two months and remained so for a full year of diversion (Dewson *et al*. 2007a, b). Four other N.Z. streams of differing character also showed divergence in riffle assemblage composition above and below streamflow abstraction points (Dewson *et al*. 2003). In a perennial English stream, the post-drought invertebrate community diverged increasingly from the pre-drought one even once flow resumed, until it was finally reset by winter high flows (Ledger and Hildrew 2001). Although in the perennial Little Stour River, U.K., there was moderate overlap between assemblages from times of normal flow and multiple periods of severely reduced flows with drought, there were discernable effects of the latter disturbance events on assemblage composition and recovery trajectories (Wood and Petts 1994, 1999; Wood *et al.* 2000).

Importantly, as in the present study, in several others where low-flow disturbance appeared not to generate substantive changes in overall assemblage composition from that at natural low flows, there were still detectable shifts in different taxonomic components comprising the assemblage (Section 7.1.3). For example, in a section of a Hong Kong river subjected to major flow diversion, despite the overall community composition of the flow-impacted reach remaining fairly similar to that of the upstream perennial section, certain taxa showed distinctly altered patterns of abundance (Dudgeon 1992b). Although divergence in riffle assemblage structure from that of unimpacted assemblages was significant in only one of the three experimentally diverted N.Z. streams, Kiriwhakapapa, various individual taxa and functional groups showed markedly altered densities (Dewson *et al*. 2007b).

General patterns in invertebrate diversity at low flows

Patterns of assemblage diversity in relation to temporal variability in natural low flows were complex, with individual river or within-reach influences on diversity sometimes precluding the identification of generalised responses. Importantly, the trends reported here integrating natural mid-dry season conditions (as well as those with artificial flow reduction) were also not necessarily matched when diversity indices were examined directly in relation to instantaneous discharge overall (Section 8.5). While a lack of coincidence in the timing of invertebrate diversity peaks or troughs suggested that assemblage composition was quite dynamic, some stability during the natural low-flow hydrograph was apparent for mean total numbers of families and taxonomic richness, relative to other diversity measures. A significant seasonal response of elevated figures for these metrics early in the low flow period occurred in only the least hydrologically predictable river. Measures of average total abundance and evenness were more site-dependent, with less consistency across rivers or over the natural low-flow period. Shannon-Wiener diversity was also temporally variable for certain rivers, yet spatially relatively consistent within each reach.

The number of species present in a stream reach has been considered more stable with flow and over time than density (Minshall and Petersen 1985; Death and Winterbourn 1994), therefore potentially serving as a more useful indicator of invertebrate response to disturbance than numbers of individuals in the long-term (Miller and Golladay 1996). Total density, in contrast, was felt to be a more useful variable for short-term or population responses.

Almost all diversity indices showed increases, though none significant, with natural flow reduction to lowest levels midsummer, across river reaches and for all biotopes (except for richness and evenness in runs). The greater diversity so often characteristic of riffle fauna as compared with invertebrate assemblages from other mineral patch types (Orth and Maughan 1983; Brown and Brown 1984; Pridmore and Roper 1985; Statzner *et al*. 1988; Brown and Brussock 1991; Palmer *et al.* 1991; Tharme and King 1994; Wohl *et al*. 1995; Gippel and Stewardson 1998; cf. Miller and Golladay 1996; Growns and Growns 2001) was most often sustained at naturally lowest flows. Riffles generally possessed higher numbers of families and corresponding richness, total numbers of individuals and Shannon-Weiner diversity than runs or, even more so, pools. Evenness, in contrast, though more similar across biotopes was highest for runs, and lowest for riffles as the most hydraulically variable biotope (Section 6.4), as also found in the perennial U.S. Brier Creek (Miller and Golladay 1996). Riffle assemblages were found to be highly variable in composition and distribution even within a single small riffle in Salem Creek, Canada (Godbout and Hynes 1982).

Components of diversity may respond differently to the same or different disturbance effects, complicating the understanding of a response (Niemi *et al.* 1993; Death and Winterbourn 1995). While this was experienced here, unnaturally severe discharge reduction led to converse responses in diversity from natural in more than 70% of the different relationships examined. Declines in diversity across various indices, though not always significant, are common, and in response to widely differing degrees and types of low-flow disturbance in perennial rivers (Hynes 1958; Ward 1976; Iversen *et al*. 1978; Extence 1981; Wright and Berrie 1987; Chessman and Robinson 1987; Hooper and Ottey 1988; Delucchi 1988; Dudgeon 1992b; Wood and Petts 1994, 1999; Bickerton 1995; Pollard *et al*. 1996; O'Keeffe and Uys 1998; Cazaubon and Giudicelli 1999; Rader and Belish 1999; Wood *et al*. 1999; Davies *et al*. 2000; Caruso 2000; Ledger and Hildrew 2001; McIntosh *et al*. 2002, 2008; Dewson *et al.* 2003, 2007a). Where changes in diversity in relation to abnormal flow reduction were inconsistent in the present study, it commonly reflected different directions of response among hydraulic biotopes, a factor seldom considered in low flow investigations (see also Section 8.5). This supported the need to examine responses by biotope type and with explicit recognition of the patchiness of flow effects within the riverscape.

Total number of taxa was the most consistent measure of invertebrate response to low-flow disturbance of all diversity indices. Artificial flow disturbance reduced the mean numbers of families below those of unimpacted assemblages during the lowest flow months across biotope types, most notably for riffles, and for all flow-disturbed rivers. However, declines were neither significant nor proportional to streamflow

diversion magnitudes. With responses aggregated across all flow-impacted reaches, extreme flow reduction also depressed family richness in all biotopes, leading particularly to increased taxonomic conformity between riffles and runs; greater variability in response was apparent for different biotope patches in individual reaches. In comparison with the present study, mild baseflow diversion of 25% in St. Louis Creek mainstem did not alter riffle taxon richness (or abundance) or its spatiotemporal variation from that of unimpacted upstream assemblages, although near-total baseflow reduction in a tributary, West St. Louis Creek, reduced species richness by 16% (and total density by 50%) relative to upstream controls (Rader and Belish 1999). The number of riffle taxa and five other diversity indices showed no significant once-off effects of discharge reduction downstream of points at which 28-98% of flow was being abstracted on four N.Z. streams (Dewson *et al*. 2003). Similarly, numbers of riffle taxa did not change in response to artificial flow reductions of 89% to above 94% for one month, in three New Zealand streams, and remained unchanged by two months of severely reduced flows in near-natural Reef Creek (although shifts in other biotic measures occurred; Dewson *et al*. 2007a, b). In the slightly anthropogenically impaired Kiriwhakapapa Stream, subjected to the least streamflow diversion, however, riffle taxon richness was the only diversity measure to decrease significantly, in the second month. The absence of changes in diversity indices in the more polluted Booths Creek, despite it being subjected to the greatest discharge reduction, was attributed to a naturally more tolerant community and the fact that suitable hydraulic conditions persisted for riffle dwellers.

While the trend in numbers of taxa in the present study suggested at least some localised loss of taxa from impacted reaches, there was no evidence to support the local extirpation shown in some cases (Hynes 1958; Larimore *et al*. 1959; Iversen *et al*. 1978; Extence 1981; Ladle and Bass 1981; Canton *et al*. 1984; Delucchi 1988; Pollard *et al*. 1996; Rader and Belish 1999; Ledger and Hildrew 2001; Caruso 2002; Dewson *et al*. 2003; McIntosh *et al*. 2002; 2008). For instance, a few invertebrate taxa were absent in severely flow-altered reaches below major water diversions on the perennial Hawaiian Iao and Waihee streams, including an endemic shrimp that prefers fast-flowing habitats in the latter stream (McIntosh *et al*. 2002; 2008). Eleven dominant species of various families were locally eliminated by ten weeks of severe low flows with drought, in a Welsh mountain stream (Hynes 1958), and with more protracted low flows in the perennial West St. Louis Creek, U.S.A., ten taxa abundant upstream of a diversion were absent downstream (Rader and Belish 1999).

Taxa previously not observed or locally rare have also appeared in response to extremely low flows (Hynes 1958; Harrison 1966; Extence 1981; Canton *et al*. 1984; McAuliffe 1984; Lake 1989; Boulton and Lake 1992b; Pollard *et al.* 1996; Rader and Belish 1999; Ledger and Hildrew 2001; Dewson *et al.* 2003). Previously uncommon taxa became well established during the low flow months with drought-induced flow reduction in Trout Creek, a perennial Colorado mountain stream, including Hydracarina, *Ablabesmyia* sp., oligochaetes and a plecopteran (Canton *et al*. 1984). Previously unrecorded chironomids, *Polypedilum* sp. and *Stempellinella* sp., and a leptophlebiid mayfly were found post-drought in a perennial English stream, as

well as a chironomid species able to exploit disturbed temporary habitats (Ledger and Hildrew 2001). In contrast, there was no substantive evidence of the appearance of such taxa in the present study, although a few impacted assemblages did include high numbers of recently hatched young instars (tanypod and coleopteran larvae) probably of taxa already present. This suggested either enhanced reproduction (Extence 1981) or possibly, as observed in Scottish streams after summer drought, recolonisation from desiccation-resistant eggs or adult oviposition (Morrison 1990).

Less consistency in assemblage response was apparent across the flow-disturbed rivers and biotopes for numbers of individuals, assemblage evenness, and Shannon-Weiner diversity, than for taxon number or richness. Such inconsistency appears commonplace with natural and artificial dry-season flow reductions within and among perennial rivers elsewhere, and in several instances was attributed to shifts in the abundances of specific taxa (e.g. Castella *et al*. 1995; Rader and Belish 1999; McIntosh *et al*. 2002; Dewson *et al*. 2003; Section 7.1.3). For example, marked increases in abundances of rheophilous families particularly (cf. decreases in a few families, notably Hydropsychidae) occurred in the upland Truim River, U.K., in response to artificial flow reduction and physical habitat changes, while the Garry River generally experienced decreased abundances (Castella *et al*. 1995). In another local river, the Ashope, even dramatically flow-altered river conditions did not trigger any detectable density shifts.

In this study, with discharge reduction below historical minima, the mean total numbers of individuals exceeded those at natural low flows for riffles particularly, and runs (see below for the likely mechanisms involved). This result was one of few for diversity that was entirely complemented by direct discharge-abundance trends (Section 8.5). Increases in total densities with low flows have been reported elsewhere (Extence 1981; Wright and Berrie 1987; Rader and Belish 1999; Dewson *et al.* 2003, 2007b), although declines in abundances seem more common (Hynes 1958; Iversen *et al.* 1978; Ladle and Bass 1981; Cowx *et al.* 1984; Canton *et al.* 1984; Hooper and Ottey 1988; Wood and Petts 1994, 1999; Pollard *et al.* 1996; Rader and Belish 1999; Cazaubon and Giudicelli 1999; McIntosh *et al*. 2002, 2008; Section 7.1.3). Artificial flow reductions in four different N.Z. streams generally resulted in increased average abundances for riffle taxa, including Elmidae, *Deleatidium*, Orthocladiinae and *Aoteapsyche* (Dewson *et al*. 2003). Experimental, major discharge reductions for one month led to consistently higher than natural dry-season total densities of riffle invertebrates in three New Zealand streams (Dewson *et al*. 2007b). Increases varied from 33 to 59%, regardless of similar reductions in total wetted habitat, possibly due to unquantified losses in relative riffle area. The five most common riffle taxa in each stream also increased in abundance, with a maximum increase, 851%, for the leptophlebiid, *Austroclima sepia.* A lengthier period of lesser baseflow diversion of 40% in St. Louis Creek, U.S.A., led to a 57% increase in invertebrate densities, with especially pronounced ephemeropteran and plecopteran numbers (Rader and Belish 1999); the response was attributed to elevated temperatures as, unlike in the current study (Section 6.3), wetted perimeter did not substantially decrease with discharge reduction.

A noteworthy consequence of the patchy fragmentation of wetted habitat was dramatically elevated variability in the numbers of individuals immediately experimental flow diversion was initiated, with both highest mean densities of individuals and very low abundances encountered in one of the two most flow-impacted locations. The result highlighted a possible role of extreme low flows in increasing benthic variability. Near-total flow diversion in West St. Louis Creek, U.S.A., also led to significantly increased variability (CVs) in total invertebrate density and number of taxa, of 33% and 63%, respectively, in downstream flow-impacted reaches relative to upstream, though in periods of frequent flow fluctuations (Rader and Belish 1999); the pattern was similar, though not significant, in the completely diverted East St. Louis Creek. Similar variability in local invertebrate abundances (and spatial patch heterogeneity) have been recognised features of other flow disturbance studies (e.g. Lancaster and Hildrew 1993a, b; Hart *et al*. 1996; Lake 2000; Konrad *et al.* 2008). As Palmer *et al*. (1997) and Lancaster and Belyea (2006, p. 792) observed "Potentially valuable ecological information about other limiting factors lies in the scatter or variance of abundance-environment relationships, but it is often ignored or viewed as an annoyance by ecologists in pursuit of a mean value or central response." There is an increasing need to more closely examine such variance, in addition to measures of central response, with flow disturbance effects, and to explore the value of low flow variability as a quantified biophysically relevant metric, rather than as statistical interference, in characterizing invertebrate response to altered lotic conditions.

Shannon-Weiner diversity was consistently maximised under natural low flows midsummer, and for all biotope types. Conversely, this measure of diversity tended to be lowered with artificial flow reduction and particularly for riffle assemblages (Section 7.8.2). Changes in evenness, though more difficult to generalise, were obviously strongly connected to biotope type (see also Section 8.5). While assemblage evenness increased within riffles and pools with flow reduction to naturally low levels, a general decrease in evenness in runs at both natural and artificially extreme low flows pointed to various shifts in invertebrate dominance for this patch type. Shannon-Weiner diversity also decreased with extremely low summer flows, due to drought, in the upper perennial reach of the English River Lambourn (Wright and Berrie 1987). Slightly reduced riffle species diversities (Simpson's index) were detected below different magnitude flow diversions on the Tukipo and Tamaki rivers and Mangaterere and Raparapawai streams, N.Z. (Dewson *et al*. 2003). In contrast, Simpson's diversity and riffle species evenness (among several other diversity metrics) were effectively unaltered by artificial flow reductions from 89 to above 97%, of one month to a year, in three other New Zealand streams (Dewson *et al*. 2007a, b).

Invertebrate persistence with exposure at low flows

Generally speaking, despite shrinking wetted margins and fragmentation of in-channel habitat (Chapter 6), invertebrate stranding and mortality were low, regardless of the magnitude of flow reduction or the degree of streambed exposure. These findings were corroborated by other low flow studies in perennial rivers where stranding was not marked, and the majority of invertebrates appeared able to rapidly relocate to more suitable areas (Moon 1956; Extence 1981; Corrarino and Brusven 1983; Jensen and Jensen 1984; McIntosh

et al. 2002, 2008; Dewson *et al*. 2007a). Although most benthic invertebrates were not stranded as water levels receded with extreme low flows in the River Roding, U.K., a number of species were not able to migrate easily and desiccated post-stranding (Extence 1981). For instance, prosobranch molluscs and the predominantly sessile cased trichopterans, *Athripsodes aterrimus* and *Hydroptila tineoides*, were locally largely eliminated, while more mobile trichopterans and a pulmonate snail were unaffected. More than half the benthos avoided stranding during two manipulated discharge reductions that dewatered riffles in experimental channels on Grande Ronde River, U.S.A., although increases in stranded individuals proportional to the progressive reductions were apparent for chironomids, *Simulium* sp., and *Rhithrogena hageni* (Corrarino and Brusven 1983). Near-total stranding occurred in autumn, however, when substratum drying was rapid with high temperatures.

In the current study, in a few streambed areas exposure was sufficient to prevent even typically mobile invertebrates from reaching still-submerged substrata. As a result, very low numbers of individuals, but of a wide range of taxonomic orders and families, were found in damp exposed substratum patches and other variously dewatered microhabitats at extremely reduced flows (unpubl. data), where they appeared to persist for at least several days (though this was not possible to confirm). The ability to survive in such low flow refuges, at least in the short-term, has been documented with low-flow perturbations in other perennial rivers (e.g. Moon 1956; Hynes 1958; Iversen *et al*. 1978; Ladle and Bass 1981; Jensen and Jensen 1984; Canton *et al*. 1984; Morrison 1990; Dudgeon 1992b; Pollard *et al.* 1996; Caruso 2002). Such exposed environments presumably represented transient flow refuges at best. High numbers of elmid larvae, for example, were found using the moist grooves and pits (also reported used in Downes *et al*. 1998b) of stones exposed by flow reduction, but were also observed actively vacating such drying stones in one of the impacted reaches. Elmidae (notably *Stenelmis*) were found to be adaptable under extreme low flows in the case of a largely perennial stream, Smiths Branch, U.S.A., and able to tolerate habitat exposure, desiccation and standing waters (Larimore *et al*. 1959). In addition to other aquatic coleopterans and mayfly nymphs, they persisted in the moist substrata of exposed riffles, but not with prolonged drying. Several other mobile invertebrates were observed to relocate across the drying streambed to moist or wetted habitats. *Helodes* sp., a member of the Helodidae family which is well adapted to inhabiting damp substrata, was abundant in the exposed streambed during periods of extreme low flows, with diversion in a perennial stream reach (Dudgeon 1992b). Although hydropsychids are also known to tolerate exposure in moist sediments, for up to 30 days following streambed dewatering (Imhof and Harrison 1982, cited in Dudgeon 1992b), they did not persist in substantial numbers in the same reach. With artificial flow reductions in the Gudenaa River, most invertebrates, including mayflies and stoneflies, avoided stranding by active swimming into the flowing part of the channel (Jensen and Jensen 1984). Even most individuals of species susceptible to stranding (burrowing taxa and cased trichopterans) were still able to relocate under very low flows or exposure. The mayfly, *Ephemera danica*, was able to survive by leaving its burrows with the first sign of declining water levels or by crawling over the exposed bed to reach water, once flow reduction had occurred. It was also the only taxon remaining alive in bed sediments, albeit in very low numbers, four days after bed drying. With low flow conditions in a

small, intermittent U.S. stream, Rock Riffle, that naturally experienced rapid transitions from flowing water to a near-dry bed with isolated pools, several insect taxa were observed crawling to still-wetted habitat patches, while others sought refuge in rock crevices (Stehr and Branson 1938).

Individuals of a few families, including Leptophlebiidae and other mayflies, were found moribund or dead in moist sediments along the desiccated river-margins and previously submerged riffle patches, or around the wetted edges of pool and run boulders where water levels had markedly declined (pers. obs.; the last outcome was also observed by Larimore *et al*. 1959). These isolated incidences were more likely due to exposure on stranding than failed emergence attempts, though occasional emergence episodes were observed and have been reported elsewhere during such flow conditions (Ulfstrand 1967; Fisher *et al*. 1982; Boulton and Lake 1992a). Although it could not be assumed that exposed animals were not consumed by terrestrial or aquatic predators or scavengers (Stehr and Branson 1938; Moon 1956; Larimore *et al*. 1959) or decomposed too rapidly for detection (Moon 1956), neither living nor dead animals were recovered from totally dry substrata (unpubl. data). Such habitats are typically hostile for invertebrates, unless taxa have appropriate life cycle traits that facilitate persistence (e.g. Larimore *et al*. 1959; Harrison 1966; Iversen *et al*. 1978; Canton *et al*. 1984; Cowx *et al*. 1984; Morrison 1990; Feminella 1996; O'Keeffe and Uys 1998; Boulton 2003; Lytle and Poff 2004). For instance, in four small, summer drought-affected Scottish streams, streambed areas devoid of flowing water contained no living aquatic invertebrates, but dead desiccated individuals were observed (Morrison 1990). As a result of bed desiccation with drought intermittency in a Welsh mountain stream, Afon Hirnant, there was direct evidence of stonefly nymph mortality and no living invertebrate individuals were encountered in upper substratum layers (Hynes 1958).

Potential for drift with flow reduction

Drift was not quantified in this study, but appreciating the varied drift relationships found with discharge and habitat reduction, it is probable that drift density and/or rate intensified above natural levels in response to low flow stress for some taxa within locally disturbed streambed areas and, less likely, decreased for others (Minshall and Winger 1968; Pearson and Franklin 1968; Corkum *et al.* 1977; Corrarino and Brusven 1983; Perry and Perry 1986; Brittain and Eikeland 1988; Poff and Ward 1991; James *et al.* 2008, 2009; Section 7.1.3). While benthic sampling was undertaken within a maximum of three days following experimental flow reduction, drift responses in that same time period might have gone undetected (Perry and Perry 1986; Poff and Ward 1991; James *et al.* 2008, 2009); immediate catastrophic drift was not obvious. For example, although total drift density only increased significantly in the New Zealand stream in which flow reduction was most extreme, drift densities for several common taxa increased sharply within three days of experimental flow diversion (of 80% and above) in all three local streams, before declining to near-natural levels (Chironominae were an exception with a weak but sustained drift response) (James *et al*. 2009). The rheophilic hydropsychid, *Orthopsyche* sp., and filter-feeding mayfly, *Coloburiscus humeralis*, for instance, increased in the drift in the first two days of extremely reduced flows.

Rates of change in discharge at both the start and end of the manipulated flow diversions, though gradual, still exceeded natural rates, such that the possibility that they also induced drift cannot be discounted (Minshall and Winger 1968; Pearson and Franklin 1968; Perry and Perry 1986; Brittain and Eikland 1988). A gradual change in water level was considered one of the factors leading to a lesser impact on invertebrates of the Danish Gudenaa River, than an artificial discharge reduction with more rapid fluctuations that was presumed to halve the number of taxa from natural through drift (Jensen and Jensen 1984). Discharge increases of about two and a half times baseflow in U.S. experimental streams commonly triggered a threshold drift response (though not for all taxa), of on average ten-fold relative to reference streams, that was more immediate and pronounced with an abrupt rate of flow change (Imbert and Perry 2000). There was, however, no significant effect on benthic densities.

Despite these considerations, whether drift was active to relocate to areas of more preferred conditions with reduction in suitable habitat, or passive due to increased densities of individuals in the remaining wetted area (James *et al.* 2008), it was unlikely to be a major contributor to the invertebrate responses detected with low-flow disturbance. Extreme discharge reduction has been shown to limit mean drift distance, with few individuals drifting more than a couple of metres (even in patches of relatively high velocity) and most drifting invertebrates remaining in the flow-impacted reach (James *et al.* 2008, 2009). Townsend and Hildrew (1976) also found that 85% of drifting invertebrates originated less than two metres upstream when current velocities were very low. Drifting was therefore considered an unlikely option for rapid avoidance of impacts of severe flow reduction in small, shallow streams particularly, and hopping behaviour (i.e. downstream drift by means of a series of hops through a flow-disturbed reach) also potentially risky (James *et al*. 2009). Once taxa have relocated to suitable microhabitats it is also considered unlikely they would drift again, provided their nutritional and physiological needs were met (Hooper and Ottey 1998; James *et al.* 2009). In Hunt Creek, U.S.A., flow-induced drift dynamics were accompanied by simultaneous changes in median benthic densities for two common drifters (Hooper and Ottey 1988). However, in the N.Z. multiple stream study, drift increases with experimental discharge reduction were not associated with reduced benthic densities (Dewson *et al.* 2007a, b; James *et al.* 2008, 2009). In fact, differences in benthic composition increased over the low flow period, while drift propensities typically rapidly returned to natural, a result attributed to the far smaller proportion of invertebrates drifting than present in the benthos.

Clearly, there would have still been merit (resources permitting) as shown by James *et al.* (2008), to characterizing invertebrate responses to potential low flow thresholds in terms of both benthic dynamics and drift. Monitoring both components in parallel might have been especially relevant from the standpoint of recovery from low-flow disturbance. Though opportunities for recolonisation from upstream were perhaps more limited than from downstream reaches during the impact phase, an influx of individuals was possible through the non-diverted component of discharge, potentially aiding recovery (Dewson *et al.* 2003).

7.8.2 Invertebrate redistribution dynamics within the patch mosaic in response to low flows

Patchiness of low-flow disturbance

In much the same way as high flow events have been found to disturb a riverbed patchily (Doeg *et al.* 1989; Lancaster and Hildrew 1993a; Death 1996a, b; Matthaei and Townsend 2000; Matthaei *et al*. 2000; Section 1.4.6), normal and especially, extreme low flows, exerted non-uniform disturbance effects (as described in: Pickett and White 1985; Barmuta 1989; Reice *et al*. 1990; Hildrew and Giller 1994; Ledger and Hildrew 2001) on invertebrate assemblages and species populations across all river reaches and types of hydraulic biotope. As a result, individual streambed patches potentially represented quite different flow disturbance histories (McCabe and Gotelli 2000; Matthaei and Townsend 2000). With the artificial flow reductions, not all individual patches in the riverbed mosaic were affected or, when disturbed, then not equally so. Such flow-generated patchiness therefore resulted in a complex mosaic structure, with marked variations in habitat character over small distances (Beisal *et al.* 1998). Consequently, there were not unexpected localised differences in the degree of influence experienced by benthic assemblages where the disturbance was felt (Lake *et al.* 1989). Knowledge of how the size of the sampled area relates to the sizes of patches created by disturbance then becomes important, as shown for riffles of upland rivers of the Acheron Catchment, Australia, where within-site and among-river differences in invertebrate response occurred as a result of the spatially patchy way flood disturbance acted over the riverbed down to the scale of individual stones (Downes *et al*. 1998a).

Such small and locally variable flow disturbances where the entire bed is not disturbed more likely represent the redistribution of individuals rather than true recolonisation from distant sources (Hooper and Ottey 1981; Matthaei *et al*. 2000). It was clear that in this study, changes in assemblage composition and diversity from those at natural low flows were best viewed in this context. Most evidence of invertebrate response with low-flow disturbance could be logically explained in terms of the dynamic redistribution of individuals in relation to the individual physical characteristics, spatial configuration and connectivity of different streambed patches with progressive alteration in flow states. Benthic invertebrates naturally exhibit a pattern of continual small-scale patch redistributions in rivers in response to season, discharge (Lancaster *et al*. 1990; Winterbottom *et al*. 1997) and the wide variations occurring in hydraulic habitat factors over small patch areas (Ulfstrand 1967; Hart *et al*. 1996). Here, the first clear evidence of biological effects of low-flow perturbations emerged at the scale of assemblages from different hydraulic biotopes within the patch mosaic, though natural variability in invertebrate composition remained a complicating factor at this habitat scale (Minshall and Petersen 1985).

Appropriate patch units for examining invertebrate response to low-flow disturbance

The occurrence of a species within the assemblage of a certain mesohabitat or finer patch unit (Section 1.4.8) indicates that it possesses traits, including those tied to disturbance response, suitable for the habitat

conditions it encounters at this scale, as well as for the higher-level, spatially nested landscape filters (e.g. flow variability at basin scale, reach-scale channel hydraulics) to which it has been exposed (Death 1996b; Poff 1997; Lytle and Poff 2004). In this thesis, for all river reaches, stratification of physical habitat at hydraulic biotope and nested microhabitat scales was effective in revealing distinct associations among invertebrates and various habitat patch units. This created expectations of varying degrees of low-flow sensitivity and tolerance to changing local habitat conditions among individual families and species (supported in Sections 8.3 and 8.4) and thus, differences in response to the same unit of flow disturbance and its effects on patch conditions (Whittington 2000).

Differentiation of assemblages based on biotope type as a spatial unit was more apparent than any natural month-to-month changes in composition (and by implication, low flow regime) or location effects, beyond the basic natural patterns previously described for the study rivers. In the Nantahala Basin, U.S.A., associations of invertebrate functional groups in each of four hydraulically distinct habitat types were consistent across multiple river sites of differing physical and chemical character, suggesting that at the spatial and temporal scales investigated habitat types maintained their functional integrity (Wohl *et al.* 1995). Moreover, similarities in composition were greater across different habitat types than for sites or subcatchments. Greater differences in benthic community structure between adjacent riffles and pools, than between permanent and temporary riffles across a flow permanency gradient, in four streams in the same New York catchment, U.S.A. (Delucchi 1988), similarly suggested that the influence of the biotope could be at least as strong as effects due to differences in temporal flow regime.

That differences in biotope composition held across a multiplicity of scales supported the relevance and robustness of the hydraulic biotope (demonstrated to be a hydraulically meaningful entity in Chapter 6) from an ecological perspective at low flows. It also supported biotope transferability across rivers, as originally supposed by Wadeson (1996) and Padmore (1997). The affinities of specific taxa for particular hydraulic biotopes in relation to low flow state, as well as the direct relationships between patch hydraulic factors and measures of invertebrate response, lent further support to these findings (Sections 8.3, 8.4 and 8.8). Working at the finer resolutions of flow type and species level, King and Schael (2001) similarly concluded that the hydraulic biotope was an ecologically meaningful geomorphic unit for invertebrate study.

The natural stability of the low-flow period afforded invertebrates more opportunities to associate themselves with specific biotopes and microhabitats than perhaps at other times of the year (Poff and Ward 1991). In every river, there were significant natural differences in invertebrate assemblage composition among biotope types. Some five to nine families effectively characterized the dominant riffle, run and pool biotopes under natural low flows (based principally on relative abundances rather than presence/absence), occasionally with a different family best representing the same biotope in different rivers. Of the few families that were consistently useful indicators of biotope type and hence patch flow-mediated hydraulics, however, only Simuliidae, as a recognised obligate rheophile (O'Keeffe and Dickens 2000; Growns and Growns 2001;

O'Keeffe *et al.* 2002), effectively differentiated among all types. Other key families with potential as natural low-flow indicators formed two main groups, with the greatest number of potentially flow sensitive taxa from riffles (e.g. Elmidae and acarinids). Indicator taxa in the second group (e.g. Leptoceridae, Teloganodidae and Caenidae) were naturally most abundant in pools. Similarly, several chironomids were clear discriminant species for biotope type at natural low flows, again with the highest number in riffles (e.g. *Rheotanytarsus fuscus*, *Notocladius capicola* and *Rheocricotopus capensis)*. Only the predatory tanypod, *Paramerina*, was a consistent indicator of pool environments. Tanypods have been shown to be common benthic predators in pools at low flows (e.g. Boulton and Lake 1992a). Although a number of other taxa exhibited potential as biotope indicators at low flows, they showed greater natural overlap across biotope types or less cross-river consistency.

Riffles and pools were clearly differentiated by naturally higher densities of Hydropsychidae, Simuliidae and Chironomidae in the former biotope. Lesser differences in faunal composition between riffles and runs (see also Pridmore and Roper 1985), and between pools and runs, mirrored the relative hydraulic similarity between these biotope pairs (Section 6.4). Riffles and runs could, however, be differentiated from each other by Simuliidae, Philopotamidae and, less consistently, baetids, which all tended to be more abundant in riffles. Runs were best differentiated from pools by higher densities of Chironomidae (with stronger associations of particular species than for the family) and simuliids. Pools exhibited the lowest internal faunal similarities of all biotopes, possibly reflecting the diverse sets of pool conditions encountered during the dry season (Sections 5.3, 6.4 and 6.5). While the dominant biotope-associated families (Baetidae, Chironomidae and Simuliidae) were represented by a relatively wide species range, within the Chironomidae at least, species populations seldom contributed information on direct responses to flow additional or contrary to that apparent at family level. Moreover, for most other families indicative of biotope type, a single genus (e.g. Philopotamidae were represented by *Chimarra* spp.) or low numbers of species (e.g. two *Cheumatopsyche* spp.) represented the family (Chapter 2). These considerations, as well as the results of this and other studies (e.g. Pardo and Armitage 1997; Kay *et al*. 1999), indicated that family taxonomic level was generally sufficient to reveal flow-related biotope use and flow disturbance response. The importance of additionally considering species individually, due to within-family species differences in habitat and life history attributes, is acknowledged. For example, responses to drought-reduced summer flows by species within the same taxonomic group differed for the Simuliidae in Waterston Stream, U.K. (Ladle and Bass 1981). Increases and decreases in the abundances of *Simulium ornatum* and *S. vernum*, respectively, were postulated to be due to factors such as life history attributes, food quality, substratum condition and selective predation.

The natural affiliations of benthic assemblages for different biotopes, and demonstrable presence of indicator taxa, highlighted the influence hydraulic factors might be expected to exert in invertebrate response to changing low flows. Numerous other studies have similarly reported varyingly distinct, natural invertebrate-mesohabitat associations with taxa indicative of particular mesohabitat types and their underlying hydraulic

conditions, for individual or multiple rivers (Sheldon and Haick 1981; Logan and Brooker 1983; Pridmore and Roper 1985; Barmuta 1989; Palmer *et al.* 1991; Boulton and Lake 1992a; Scarsbrook and Townsend 1993; Armitage *et al*. 1995; Wohl *et al.* 1995; Grundy 1996, cited in Newson and Newson 2000; Pardo and Armitage 1997; Beisal *et al.* 1998; Tharme and King 1998; Kay *et al*. 1999; Wood *et al*. 1999; Tickner *et al.* 2000; Choy *et al.* 2000; Buffagni 2001; Brunke *et al.* 2001; Section 8.1). For instance, Elmidae were found to be most strongly associated with 'gravel fast' and 'gravel slow' mesohabitats, while Oligochaeta were most common in 'silt' across 11 mesohabitats in Mill Stream, England (Armitage *et al*. 1995). For three New Zealand streams, of nine major taxonomic groups recorded, only Ephemeroptera were consistently more abundant in riffles, whereas Gastropoda and Amphipoda were naturally at higher relative abundances in runs (Pridmore and Roper 1985).

Emerging signals of low-flow perturbation from biotope assemblages

The varying hydraulics of streambed patches at very low flows provided a suite of refugia (*sensu* Lancaster and Belyea 1997; Section 1.4.3) from low-flow disturbance (Hildrew and Giller 1994), of differing degrees of access and suitability for the persistence of different biotope-affiliated taxa (Gore 1998; Lancaster and Belyea 2006). As biotope patches sequentially underwent hydraulic transformation with progressive flow reduction (Section 6.5), shifts in assemblage composition occurred across the same biotope continuum, lending support to Boulton's (2003) observation that composition might alter in response to shifts in the availability of different habitats, rather than reflecting tolerances to flow events *per se*. Coupled with this dynamic redistribution of the benthos across different biotope patches, with chironomid species' responses according well with those at family level, there was evidence of within-patch redistribution down to the microhabitat scale of individual stones (Section 7.8.3). Differences in the degree and direction of change in assemblage composition were apparent for riffles, runs and pools, and while not possible to demonstrate, might have partially counterbalanced one other, somewhat obscuring response patterns.

Across the flow disturbed reaches, these direct responses by invertebrate assemblages provided the first evidence that although the hydraulic integrity of individual biotopes intensified with extreme flow reduction (albeit with different combinations of hydraulics influential that at normal flows; Section 6.3.2), their representative biological integrity weakened across the patch mosaic. This tendency was already evident at naturally lowest flows, where biotopes were typically more faunally similar to one another, at least at family level, than at other times over the dry season; chironomid biotope specificity was only occasionally amplified at natural low flows. While within a few patches invertebrate assemblage-biotope affinities were retained even at extremely low flows (at family and species levels), in most instances they were eroded. The break-down of biotope affinity was often incomplete, but where total loss of biotope-assemblage associations occurred across the riffle-pool continuum it was indicative of major flow disturbance (as confirmed by examining in greater detail the individual taxa and hydraulic factors implicated; Sections 8.3 and 8.4). This provided firm backing to the postulate of Palmer *et al.* (2000, p. 563) that "flow-induced movements of patches and of fauna could decouple habitat characteristics and faunal habitat preferences", with implications

for the extent to which faunal response to low-flow disturbance could be unequivocally related to specific patch types and their spatial arrangement.

In contrast to the present study, most assessments of low-flow disturbance in perennial rivers have seldom differentiated among responses for multiple biotopes (or other mesohabitats), this despite widespread recognition of mesohabitat-invertebrate associations and their ecological significance (Section 8.1.1). Instead, they have typically focused on the biota of a single patch type, commonly riffles, or on contrasting riffles and pools (Section 7.1.3). Much of the evidence of invertebrate response to low flows is therefore fairly generalised at reach scale, rendering direct comparisons difficult. The breadth of information useful for understanding patterns of assemblage responses at low flows in relation to the most plausible underlying mechanisms is also constrained in this way. Although these limitations also increase the probability of a mix of responses in assemblage measures within a single river, it is acknowledged that in this study, a degree of inconsistency in invertebrate trends was encountered regardless.

Transformations in assemblage composition with severe flow reduction appeared in large part due to the movement of invertebrates out of preferred habitats and into hydraulically (or otherwise) altered patches of marginal suitability, with wetted habitat reduction and fragmentation (Chapter 6). Hooper and Ottey (1982) similarly considered variations in benthic composition likely due to high rates of invertebrate exchange among habitats during short-term low flows. It has been previously posited that relatively mobile invertebrate taxa should be able to behaviourally track discharge-mediated hydraulic change in this way, with their microdistributions rapidly responding to stream-wide hydraulic conditions, and with distribution patterns reflecting contemporaneous (rather than antecedent) flow conditions (Hooper and Ottey 1982; Davis and Barmuta 1989; Lancaster and Belyea 2006). Though yet to be rigorously tested, this supposition appeared valid across multiple rivers at low flows in the current study. Few studies have explicitly related invertebrate assemblage or taxon responses to patch dynamics driven by flow disturbance (Armitage *et al*. 1995), but shifts in the distributions of invertebrate taxa in relation to changes in habitat hydraulics have been reported under variously altered discharge patterns (Hooper and Ottey 1982; Wetmore *et al.* 1990; Dudgeon 1992b; Lancaster and Hildrew 1993a; Armitage 1995; Imbert and Perry 2000; Rempel *et al.* 2000). For instance, patterns in community structure that reflected flow sensitivity and hydraulic preferences corresponded closely with spatial patterns in hydraulic habitat in the Fraser River, Canada, at different discharges (Rempel *et al.* 2000). Following varying flow increases, redistribution of benthic invertebrates across the wetted streambed was demonstrated in experimental streams off the Mississippi River, U.S.A. (Imbert and Perry 2000).

Invertebrate susceptibility to low-flow perturbations in this study, in terms of relative ability to respond through habitat redistribution, was clearly influenced by the mobility of taxa and the extent to which that was hindered by low water levels and current velocities (Lancaster *et al*. 1990). Many invertebrate taxa are highly mobile and able to move over a large number of patches (substratum areas of a few hundred cm^2) in

their lifetimes (Winterbottom *et al*. 1997). Those that actively walk about on the substratum are considered less likely to be affected by changing flow conditions that those more reliant on drift (Lancaster *et al*. 1990). A series of patch-scale field colonisation experiments in Broadstone Stream, England, demonstrated how the mobility of the vast majority of taxa was discharge dependent and was enhanced as discharges increased, influencing their natural, continual microdistributions (Winterbottom *et al*. 1997). Solely the stonefly, *Nemurella pictetii*, showed greatest mobility at summer low flows, but even then with a weak correlation between the mobility index of Lancaster *et al*. (1990) and discharge.

Invertebrate response pathways and patterns at biotope scale

Invertebrate responses for riffles

Two main paths of invertebrate response were common in relation to the dramatic reductions in riffle patch availability, connectivity and hydraulic character recorded in all reaches subjected to artificial discharge reductions (Sections 6.5 and 6.7). The first was the packing of individuals, particularly of rheophilic taxa, within riffle patches. The second pathway involved the movement of individuals of various taxa from riffles into other tolerable or more suitable patches. Members of several riffle-dwelling families relied on both such responses, depending on the conditions within the affected individual riffle patch compared with those of neighbouring habitat patches of the same or different types (as corroborated in Chapter 8). Although there were no detectable effects on riffle composition of discharge reduction that approximated historical dry-season minima, despite loss of preferred habitat, divergence of assemblages of flow-impacted riffle patches from those experiencing natural low flows was evident once flows were reduced well below such minima.

The compositional character of many riffle patches effectively intensified at extremely low flows, through the increased packing of obligate rheophiles and other common riffle-dwelling taxa into the diminished riffle area overall, and of individual patches; this increased the dominance by certain families, a converse trend from that recorded when water levels declined naturally midsummer. The habitat shrinkage and resultant localised crowding resulted in mean total numbers of individuals exceeding those at natural low flows (and not only for riffles, but also runs), though with high variability among patches. Exceptional was the more than doubling of simuliid densities from natural where larvae were concentrated in small remnant riffle patches to maximise, as far as possible, their preferred physical conditions. Though highly confined, and experiencing reduced velocities and films of water in the order of millimetres over stones, individuals repositioned themselves so as to remain evenly distributed. This spacing behaviour, experimentally demonstrated for simuliids in response to changing flows and local hydraulics (Chance and Craig 1986; Fonseca and Hart 1996), and also shown in relation to net positioning in hydropsychids (Edington 1965), is required to maximize filter feeding. Survival of invertebrates under such conditions requires a tolerance of such increased densities, as well as of accompanying biotic interactions which likely intensify both among individuals and between species (Extence 1981; Lancaster *et al*. 1990; Feminella and Resh 1990; Lancaster and Hildrew 1993a; Dudgeon 1993; Pollard *et al*. 1996; Section 7.1.5). These kinds of behaviours at low

flows are seldom considered even though, as Dewson *et al.* (2007c) commented, they point to potential mechanisms underlying patterns of assemblage-level response.

Such accumulations of individuals in the remaining wetted area (including through active movement from desiccated areas by more mobile taxa), reflected as localised increases in densities, is considered a primary response to short-term flow reduction (Extence 1981; Hooper and Ottey 1982; Fisher *et al*. 1982; Petts 1984; Cushman 1985; Dewson *et al*. 2007a, b; Death *et al*. 2009; Section 7.1.3). For example, localised increases in invertebrate population densities occurred in a U.K. stream, when experimental low flows lead to the contraction of fast-flowing habitat patches (Edington 1965). Patch-specific differences in water retention, and movement patterns, that led to the concentration of individuals in certain non-dry patches were contributors to the marked overall variability in riffle densities immediately before flow cessation and during the low flow period (cf. richness, which clearly declined), with periodic dry-season diversion in a perennial reach of Tai Po Kau Forest Stream, Hong Kong (Dudgeon 1992b). Leptophlebiidae, notably *Choroterpes*, Heptageniidae, Elmidae and Helodidae (especially abundant as they were additionally able to persist in the damp streambed), attained greatest densities when streamflow ceased and individuals were crowded into the few remnant habitat patches; other riffle taxa declined in abundance. Peaking of invertebrate densities (and richness) in riffles at very low flows, just before their drying and often with sharp declines thereafter, has also been reported in intermittent streams (Williams and Hynes 1977; Boulton and Lake 1992a, b; Stanley *et al.* 1994). For instance, a six-fold increase in densities preceded riffle drying in Buncombe Creek, U.S.A. (Miller and Golladay 1996).

Plausibly too, but not as obvious in this study, density increases could have reflected the proliferation of certain smaller-bodied multivoltine species with rapid development cycles and growth (e.g. chironomids, such as *Eukiefferiella* and *Rheotanytarsus*, and simuliids; Harrison 1966; McAuliffe 1984; Perry and Perry 1986; Resh *et al*. 1988), or other taxa favoured by the altered food resources and hydraulic conditions brought about by very low flows (Extence 1981; Hooper and Ottey 1982; Lillehammer and Saltveit 1984b). Increased invertebrate production at such times has also been attributed to increased hydraulic stability (Ulfstrand 1967) and water temperatures, with the latter leading to increased growth rates and stimulation of earlier reproductive activity (Extence 1981). Elevated densities of riffle individuals, below diversions removing 28 to 98% of the flow from four New Zealand streams, were ascribed to increases in the abundances of species favoured by low flow conditions, rather than to the concentration of individuals or altered resources (Dewson *et al*. 2003); there were no obvious reductions in wetted habitat. Increases in densities of the majority of species (e.g. Orthocladiinae larvae, *Hydropsyche angustipennis* and *Athripsodes aterrimus*), and significant changes in community composition, in the upper River Roding, U.K., with a marked decline in flows that led to partial riverbed desiccation and pool formation, were attributed to factors such as increased algal and detrital food supplies, and elevated temperatures (Extence 1981).

Progressive deterioration in local conditions, as wetted riffle area dramatically reduced (as compared with lower energy biotopes), its hydraulic conditions altered, and patches became increasingly exposed with continued low flows, also prompted an efflux of invertebrates from riffles (actual modes of redistribution were not investigated). Movement of benthos out of riffle patches was after lengthier lag times in the naturally more flow-variable reach, suggesting invertebrates might be habituated to variable patch flow conditions. Increased evidence of the loss of riffle individuals was also apparent in several New Zealand streams, when the duration of artificial low-flow disturbance was extended from one to upwards of two months (Dewson *et al*. 2007a, b). In the present case, emigration seemed to be into less stressful microhabitats within-patch, where feasible (e.g. deeper pockets of substratum, see below), or into adjoining patches still connected by flowing water, as invertebrate tolerances were exceeded. Most often it appeared invertebrate taxa elected the latter response, emigrating to other wetted patches that acted as temporary flow refuges, even where these were hydraulically marginal. The exceptional fragmentation and loss of riffle patches at severe low flows made it improbable that invertebrates were able to access any other suitable riffle areas (at least in the near-term), assuming they had not emigrated from impacted areas in the drift at the onset of declines in water levels (James *et al*. 2009; Section 7.8.1).

Commonly riffle fauna relocated to runs, which shared hydraulic similarities with riffles and were the dominant biotope by area at very low flows (Sections 6.4 and 6.5), but in areas of most intense local disturbance they were compelled to use pools as immediate flow refuges (as discussed below). The Hydroptilidae and Simuliidae were two of several families obliged to abandon impacted riffles for less preferred runs, in addition to concentrating in those riffle areas still able to meet their microhabitat requirements at extremely low flows. While in many riffle patches decreases in abundances also occurred for other dominant inhabitants with their redistribution, such as Chironomidae and Baetidae, in others typical inhabitants were altogether lost from assemblages with flow-induced hydraulic alteration or desiccation, among them Elmidae larvae, Acarina and Empididae. Commensurate with these effects, Shannon-Weiner diversity showed an impact signal for riffles (Section 7.8.1), with the most flow-disturbed riffles yielding the lowest invertebrate diversities. For the river in which flow diversion was highest, lower than natural riffle (and run and pool) diversities were found immediately after the disturbance, but the effect was transient with recovery before the end of the dry season.

A wide range of invertebrate groups have been found to actively leave streambed riffle patches as they began experiencing very low flows or drying in other rivers (Stehr and Branson 1938; Larimore *et al.* 1959; Kamler and Riedel 1960; Williams and Hynes 1977; Extence 1981; Hooper and Ottey 1988; Pollard *et al.* 1996). As a result of experimental flow reduction in Convict Creek, U.S.A., decreases in abundances greater than 72% relative to pre-disturbance densities occurred for four riffle species, including two mayflies observed to abandon epilithic habitats at low flows that affected velocity thresholds (Hooper and Ottey 1988). As riffles gradually became exposed, due to protracted drought in the occasionally intermittent Smiths Branch, U.S.A, taxa were observed using the receding water levels to relocate to remaining areas of wetted habitat, typically

crowding into pools (Larimore *et al*. 1959). Delucchi (1989) in contrast, found limited evidence for behavioural avoidance of drying riffles (although movement patterns differed among streams), when experimentally monitoring the movements of invertebrates before and during drying, across riffles in intermittent, temporary and perennial U.S. creeks that reflected differing degrees of flow permanence. These and various other studies (Dudgeon 1992b; Rader and Belish 1999; Dewson *et al.* 2007b; McIntosh *et al*. 2008) have additionally reported decreases in invertebrate densities and taxa that imply some degree of relocation from flow disturbed riffles. However, it is usually not made clear as to whether and how the individuals lost redistributed locally among patches.

As in this study, Ephemeroptera were sensitive indicators of extreme flow reduction in riffles in West St. Louis Creek, U.S.A., also declining in overall density (by 91%) and with many species populations showing markedly lowered abundances or, in some instances, local extirpation (Rader and Belish 1999); only *Ameletus* noticeably increased. While the majority of other taxa, including Simuliidae and certain Plecoptera, also declined with the near-total flow diversion, chironomids showed a degree of low-flow tolerance not apparent in the present study and became dominant (see also Wright and Berrie 1987; Boulton and Lake 1992b). Numbers of several riffle taxa also declined with the reduction in high velocity areas with major flow diversion in Tai Po Kau Forest Stream, among them baetids, heptageniids, *Simulium*, and even more dramatically, *Cheumatopsyche* spp., *Chimarra* sp. and Stenopsychidae (Dudgeon 1992b). At only 2% of natural dry-season flows in the upper Waihee River, Hawaii, there were significantly lower than natural riffle densities for Hydroptilidae and a rheophilic dipteran (McIntosh *et al*. 2008). Despite altered riffle availability and hydraulic quality, however, no significant differences in numbers of individuals were found for the dominant Chironomidae, or for dipteran pupae, Hydropsychidae, Trichopteran pupae, and a group comprising uncommon taxa. Densities of dominant riffle taxa, namely the filter feeder, *Orthopsyche* sp., which prefers high velocities, *Deleatidium* sp. and *Zelandobius* sp. decreased with two months of 91% discharge reduction in the near-natural Reef Creek, N.Z. (Dewson *et al.* 2007b). Similarly, in Kiriwhakapapa Stream, riffle assemblage structure was altered from natural by reduced densities of the common species, *Potamopyrgus antipodarum* and *Deleatidium* sp., as well as Chironominae and Orthocladiinae. In the limited period for which riffle patches were available, before they dried to form pools under extremely low flows in the perennial Sabie River, marked decreases occurred in total invertebrate abundance and taxon number, as well as in the numbers of rheophilic simuliids, mayflies, trichopterans and chironomids (Pollard *et al*. 1996).

As an obvious result of the dramatic loss of riffle area, the influx of invertebrates into riffle patches from the surrounding riverscape appeared rare at extremely low flows. Although a few taxa appeared as abundant young instars or for the first time in remnant riffles (e.g. juvenile coleopteran larvae, Veliidae) with low-flow disturbance in two of the diverted rivers, these occurrences may as plausibly have represented opportunistic recolonisers appearing unpredictably in such habitats for short periods of time, as an influx of individuals from neighbouring patches. In the Sabie River, for instance, the polymitarcid mayfly, *Povilla*, replaced a

more flow-sensitive species, appearing briefly once riffle hydraulic habitat had deteriorated with severely reduced flows (Pollard *et al.* 1996). Conversely, the appearance of the corixid, *Sigara dorsalis*, a species with a known preference for low velocities and lentic waters, in midstream riffle areas of the English River Roding, was speculatively due to its movement into those areas at very low discharges and associated velocities from other lower-flow habitat patches nearby (Extence 1981).

Invertebrate responses for runs

To greater or lesser degrees in all experimentally flow-altered reaches, there appeared to be either gains in taxa or individuals in the slower-flowing, but more abundant run patches, concomitant with their loss from riffles and/or similarly, losses of taxa or individuals from runs to pools. There did not appear to be suitable low flow studies for direct comparison. The most common indication of a flow-disturbance effect, demonstrable in both rivers where significant losses in riffle habitat occurred, was that run and riffle assemblages increasingly resembled each other in composition, at both family and species levels. This was principally due to gains in the abundances of taxa lost from riffle patches, among others, Chironomidae, Baetidae, Athericidae, Elmidae and acarinids. In some cases, run and pool faunas also transformed to become more alike with invertebrate redistributions. Notably, for the river reach in which least discharge was diverted, although there was no evidence of riffle taxa relocating to runs (despite marked loss of riffle habitat), impacted run assemblages from some patches closely resembled assemblages characteristic of either natural or flow-impacted pools - such pool assemblages typically possessed lower abundances of families naturally shared with runs. For the rivers subjected to the greatest discharge reductions, run and pool assemblages in some instances no longer significantly differed at family level (cf. under natural low flows and at species level, where differences were retained).

Invertebrate responses for pools

Natural variability in pool characteristics, and hence, assemblage composition (Meyerhoff and Lind 1987; Pollard *et al*. 1996; Stanley *et al*. 1997), made it more difficult to identify consistent responses of pool biota to unnatural flow reduction than for riffles or runs. Nonetheless, at very low flows, various pools showed the following patterns of response: gains in taxa or individuals from neighbouring runs or, in extreme cases, from riffles; movement of individuals of pool-tolerant and other taxa out of pools into the surrounding riverscape, or their *in situ* loss as pools became increasingly uninhabitable (shallow, stagnant, overcrowded, of degraded water quality, etc.; Canton *et al*. 1984); and/or increases in naturally pool-tolerant taxa and individuals in persistent pools. All of these responses could be related to the observed flow-disturbance driven physical dynamics of pools (Section 6.5). As water levels declined, pools and other low energy patch types became more abundant and increased in extent, relative to reach biotope proportions at natural flows, although also becoming more isolated. At the same time, while riffles decreased in availability in number and patch size, none transformed hydraulically to pools; runs showed more variable dynamics. It was not possible to differentiate instances where movement into pools might have been directly from a riffle patch, or indirectly via other patch types such as runs, though both were feasible based on reach patch mosaics. While

drift might have enabled certain individuals to avoid unfavourable pool patches (James *et al.* 2008), a factor not assessed here, as plausibly invertebrates might have been forced to utilise marginally suitable pools as flow refuges rather than risk less suitable conditions elsewhere.

Influxes of taxa and individuals from runs to pools seemed a fairly regular response to low-flow disturbance, but only with artificial discharge reduction to below historical minima did pools gain invertebrates from riffles. Significantly, riffle and pool assemblages then could not be differentiated in composition, sharing similar densities of taxa that included Elmidae, Chironomidae, Acarina, Hydroptilidae, Baetidae and Leptoceridae; this did not occur at natural low flows, when riffle and pool assemblages were highly divergent, with limited taxonomic overlap reflecting their hydraulic extremes (Edington 1965). The atypically elevated densities of elmid larvae in severely flow-impacted pools, in two of the three rivers after streamflow diversion, provided one example of this relocation of rheophiles from riffles into less suitable pool patches. The presence of this highly vagile group in a biotope they rarely utilised under natural low flows underscored the role of pools as at least temporary refugia from low-flow disturbance. Trends in taxonomic richness supported the shifts in composition with exchange of taxa between riffles and pools for one of the more intensively flow altered reaches, where pool richness increased while that of riffles simultaneously strongly decreased, suggesting an influx of taxa from drying areas. At the least flow-disturbed experimental site the converse pattern was observed for riffle richness, but pool densities more than doubled as riffle densities concomitantly decreased. This phenomenon possibly reflected a massive influx of individuals, due to the decline in high-velocity habitat required to support the naturally high invertebrate densities in the river.

In contrast to the present study, the naturally distinct assemblage structure between riffle and pool biotopes was maintained for permanent, intermittent (dry for less than three months) and dry (dry for more than three months) riffles in four U.S. New York streams at low flows (Delucchi 1988). The virtual lack of assemblage overlap suggested that riffle taxa did not migrate into pools as streams dried. In a largely perennial U.S. stream, however, a short-term intermittent spell with riffle drying to considerable depths led to the loss of taxa from riffles and the movement of many of them into pools (Larimore *et al*. 1959). In intermittent streams, peaking of invertebrate densities and numbers of taxa in pools at around the time of flow cessation has also been attributed to emigration of invertebrates from desiccating riffles (Boulton and Lake 1992b; Stanley *et al*. 1994; Miller and Golladay 1996). In the intermittent Buncombe Creek, U.S.A., after riffles dried invertebrate densities in pools more than doubled, and with 82% of that increase due to taxa that had all started to increase in densities in riffles beforehand (Miller and Golladay 1996). It was considered that periods of high reproduction coincident with drying, rather than immigration, might have accounted for increased pool densities of some taxa, in instances where pool composition was not altered during the time of riffle desiccation.

Certain instances of losses of individuals of pool-tolerant families and others in the current study were presumed to be either through emigration from or mortality within individual pools. The abiotic changes observed in many pools at extremely low discharges, including isolation over the duration of impact, were the likely reasons. In one of the most flow impacted reaches, pool assemblages experiencing deteriorating conditions had far lower densities of Caenidae, a family known to naturally prefer slow-flowing environments (O'Keeffe and Dickens 2000; Section 8.3), and an absence of ceratopogonids, when compared with pool assemblages at natural low flows. In the other severely dewatered reach, flow-impacted and natural pool assemblages diverged significantly from each other in composition during the impact phase (a pairwise effect not found in any other instance). One reason was the marked declines in abundances of four out of five taxa recorded naturally from pools, particularly water mites and baetids. Densities were also reduced for pool-dwelling Leptoceridae and Chironomidae (though with no obvious effect at species level) while Leptophlebiidae, which were in comparatively lower densities in pools naturally, became more prevalent. This last family showed no specific flow-related biotope preferences in the present study, as compared with Growns and Growns (2001) who found it a useful flow indicator. Similarly in other studies, variously isolated pools have been shown to harbour different invertebrate assemblages, which with time under low flows progressively diverged from one another in composition (Meyerhoff and Lind 1987; Pollard *et al*. 1996; Stanley *et al*. 1997).

As a result of their varied directions of faunal response, certain pools experienced a general concentration of invertebrates with shrinking habitat availability and influxes from other biotopes, while others showed a loss of individuals and taxa, possibly linked to overcrowding. Concentration of invertebrates in pools, some of which may harbour high densities of particular taxa affected by habitat fragmentation at low flows (Lake 2003), has been observed in other perennial rivers (e.g. Kamler and Riedel 1960; Canton *et al.* 1984; Pollard *et al*. 1996; Covich *et al*. 2003), as well as in intermittent streams (Stehr and Branson 1938; Boulton and Lake 1992b; Stanley *et al.* 1997). Considerable increases in densities were observed with the concentration of insect larvae in pools that formed with drought-initiated flow reduction in Świński Stream, eastern Europe (Kamler and Riedel 1960). With further flow reduction, however, pool fauna were gradually lost, with trichopterans the most tolerant of standing waters and able to survive. Mean densities of two common shrimps, *Atya lanipes* and *Xiphocaris elongata*, increased significantly during protracted low flows with drought in the upper reaches of a Puerto Rican stream, due to contraction of smaller and shallower pools that resulted in localised intense crowding and decreased resource availability (Covich *et al*. 2003). As a result of wetted habitat shrinkage, due to abnormally low water levels with a lengthy drought in Sandy Creek, U.S.A., *Procambarus spiculifer* crayfish became concentrated in isolated pools, ultimately leading to adult emigration and one population approaching local extinction (Taylor 1983). As in this study, a complex combination of invertebrate responses was triggered as riffles dried to form pools that then varyingly persisted under severe drought in the perennial Sabie River, South Africa (Pollard *et al.* 1996). Marked reductions in total invertebrate abundances and individual taxon numbers resulted, with further declines apparent immediately before the remaining refuge pools dried. Ephemeropterans and particularly

trichopterans were the first major groups to substantially decline within the refuge pools at extreme low flows, indicating a lack of tolerance of most of their composite rheophilic taxa to non-flowing conditions and habitat loss (as well as intensified predation pressure). While most mayflies eventually disappeared and freshwater mussels perished in one pool, two baetids, *Centroptilium* and *Cloeon* complex, became dominant. Dipterans and several other groups also proliferated.

An increase in lentic or pool-tolerant taxa, as observed in persistent pools by Pollard *et al*. (1996) and in several other rivers at low flows (e.g. Cowx *et al*. 1984; Boulton and Lake 1992b; O'Keeffe and Uys 1998; but cf. McIntosh *et al*. 2002), was only suggested by a change in composition for a single pool, with roughly 36% of dry-season discharge diverted. The disturbance-affected assemblage possessed high densities of corixids, a recognised pool-tolerant family (Merritt and Cummins 1984; Wright *et al.* 1984; Scholtz and Holm 1985; Picker *et al.* 2004), presumably either increasing through crowding or the production of new individuals. In contrast, chironomids, which were usually quite abundant in such pools naturally, and 11 other families, were absent. Of course, the result might simply have been an outlier reflecting the inherent variability in pool benthos.

Interestingly, one of the most apparent changes in pool composition occurred immediately after the reinstatement of natural flows in the river subjected to greatest discharge diversion. Invertebrate assemblages inhabiting previously flow-impacted pools were markedly dissimilar, at family and species levels, from all pool assemblages that had experienced natural midsummer flows. The flushing of degraded quality water from pools (Section 5.3) was possibly responsible for this effect on benthic composition. Reduced mean abundances of four of five numerically dominant groups, namely water mites, Baetidae, Chironomidae and Leptoceridae, were apparent in those pools formerly subjected to artificial flows, while Leptophlebiidae appeared favoured. Also immediately following flow recovery, only one chironomid species out of seven, *Corynoneura cristata*, was common to previously highly flow-disturbed pools and all other pool assemblages.

7.8.3 Microhabitat distribution patterns and dynamics of invertebrates at low flows

General understanding of the ways in which natural or unnatural decreases in low flow influence invertebrate distribution patterns at the microhabitat scale of individual stones, is less advanced than that of biotopes. In this study, patterns in the microdistribution of invertebrate assemblages were distinct at natural low flows, and held irrespective of month and hence implicitly, low flow regime. Moreover, assemblage composition was more strongly associated with different microhabitats than associations attributable to biotope type (for riffles and runs, pools were not examined), which suggested a central influence of microflow regime (Bouckaert and Davis 1998). Consistent with natural dry-season patterns at biotope scale though, riffle microhabitats housed more taxa and in greater densities than those of runs, except immediately below surface sediments where discharge exerts a less direct influence on hydraulics (Statzner 1981a; Davis 1986). Tops of stones were clearly a specialised microhabitat, at least at low flows, particularly in riffle

environments where they were suitable for only a few rheophilic taxa. Simuliidae were present in highest densities, followed by some members of the Baetidae. Some fifteen other taxa, most commonly chironomids, Teloganodidae and water mites preferentially utilised lower stone surfaces and the underlying substratum. While velocities are reduced in the low flow period, the distribution pattern still supported Statzner's (1981a) assertion that most taxa other than obligate rheophiles tend to be located on lower stone surfaces where hydraulic conditions are more benign.

Other studies have shown similar natural microdistribution patterns, with the preferential positions of invertebrates on the substratum influenced by a host of flow-related factors, primarily substratum architectural complexity (Ward 1976; Jowett 2003; Chapter 2) and associated microhydraulics (Ulfstrand 1967; Radford and Hartland-Rowe 1971; Corkum *et al*. 1977; Statzner 1981a; Hooper and Ottey 1982; McAuliffe 1984; Brusven 1984; Statzner *et al*. 1988; Glozier and Culp 1989; Davis and Growns 1991; Englund and Malmqvist 1996; Hart *et al*. 1996; Ledger and Hildrew 2001). The fauna associated with different parts of stone surfaces are likely responding to differing flow microenvironments, as demonstrated by Hart *et al*. (1996). For instance, differences in mean total abundance and species richness, as well as distinct microhabitat-scale front and wake communities, were associated with the microflow regimes surrounding individual riffle boulders in the Australian Serpentine River (Bouckaert and Davis 1998). Microhabitat turbulence regime and its indirect effects on local chemistry and food availability seemed to most influence the microdistribution patterns.

Flow-mediated microhydraulics clearly also played a pivotal role in the strong microhabitat specificities and related invertebrate hydraulic dependencies observed in this study (see Section 8.4). In addition to hydraulic factors *per se*, flow-linked contributors to the functional microhabitat partitioning of assemblages likely also included detrital and epilithon availability and composition (Boulton *et al.* 1988; Glozier and Culp 1989; Lancaster and Hildrew 1993a; Scarsbrook and Townsend 1993; Death and Winterbourn 1995; Jowett 2003), which differed detectably among stone microhabitats and biotopes. Differences in chironomid microdistribution have been associated with food sources, for example, with *Eukiefferiella* larvae as periphyton grazers distributed on the upper, sunlit surfaces of river stones, while *Rheotanytarsus*, a filter-feeder, inhabited both upper and lower surfaces exposed to current (McAuliffe 1984). Though not assessed here, it is acknowledged that invertebrate occupation of stone surfaces might also have been partly a function of diel behaviour patterns (Statzner 1981a; Statzner *et al*. 1988; Johnson and Covich 2000). Such diel differences in microdistribution are known for *Glossosoma pterna*, an algal grazer that inhabits stone tops during daylight hours but migrates to the undersides at night (Radford and Hartland-Rowe 1971). While *Paraleptophlebia* sp. exhibited no change in vertical distribution, Glozier and Culp (1989) found that *Rhithrogena* sp. and *Baetis tricaudatus* mayflies showed significant diel movements from lower substrate surfaces during the day, to upper surfaces at night.

Few studies have demonstrated shifts in invertebrate microdistributions (at least at individual stone scale) with flow disturbance, and then typically for floods (e.g. Hooper and Ottey 1982; Boulton *et al.* 1988; Cobb *et al.* 1992; Brooks 1998, cited in Lake 2000). For example, higher total densities of individuals and taxa were found on the undersides than tops of riffle stones in response to flooding (Boulton *et al.* 1988), and Cobb *et al.* (1992) reported *Glossosoma intermedium* selecting stone undersides during floods. Various microhabitat-scale repositioning responses of *Glossosoma nigrior* and *Baetis vagans* occurred on artificial substrates to compensate for daily discharge fluctuations, at low as well as high flows, in a small Michigan stream, U.S.A. (Hooper and Ottey 1982). The present study is one of few to explicitly address invertebrate microhabitat dynamics with artificial low-flow disturbances, and at multiple locations. Though there were no significant changes in numbers of taxa or densities for microhabitats, in response to changes from natural to extreme low flows, there were distinct shifts in microhabitat distribution patterns. These shifts comprised a fundamental element of the invertebrate redistribution dynamics observed at hydraulic biotope scale, reinforcing patterns at the landscape mosaic scale. It was unfortunately not possible, however, to ascertain the relative extent to which invertebrates redistributed among microhabitats within any individual patch or first relocated across patch boundaries. Varied invertebrate redistribution routes were characteristic for all microhabitats and, as at the biotope scale, used in a patchy manner across the streambed wherever wetted habitat was subjected to flow reduction in individual reaches.

Increases in the densities of individuals for riffle microhabitats at extreme low flows, in some cases substantiated the influence of strong microhabitat specificities superseding any unfavourable effects of increased packing of individuals, supporting biotope trends. In other instances, invertebrate shifts were a reflection of the forced relocation of individuals to less preferred biotope patches and their associated microhabitats, due to flow-related stress. This was particularly likely where artificial discharge reductions resulted in the exposure and desiccation of stones, or at least their upper surfaces (e.g. in shallow riffle patches and marginal pools), potentially intensifying hydraulic differences among microflow environments (Bouckaert and Davis 1998). Taxa then inevitably actively relocated from upper surfaces to alternative microhabitats or, presumably as local conditions deteriorated, to submerged substrata in nearby patches. In the most severely dewatered locations, relocation to less hydraulically suitable microhabitats in other patches was also driven by the loss of almost all riffle habitat. Matching findings at biotope mosaic scale, in such instances it appeared that invertebrates still endeavoured to maximise their hydraulic preferences in their new microhabitats. Yet, as extreme flow thresholds were approached or exceeded, there was a complete breakdown in microhabitat preferences in several instances (see Section 8.4).

In some intensely flow-disturbed patches, declines in the densities and numbers of riffle and run taxa normally utilising microhabitats of surface substrata were concomitant with increases in the same measures in the underlying substratum, an area liable to be sheltered from the patchy hydraulic effects of severe flow reduction. Such changes from established natural microdistribution patterns, though none significant, supported the posited role of deeper streamed areas (i.e. the shallow hyporheic zone of Boulton and Stanley

1995) acting as low flow refuges. At least limited use of underlying substrata under extreme low flows has been observed or assumed likely for perennial rivers (e.g. Wright *et al.* 1984; Perry and Perry 1986; Delucchi 1988; Wood and Petts 1994; Pollard *et al*. 1996; Ledger and Hildrew 2001), although Delucchi (1989) found little vertical penetration of invertebrates into the substratum of a permanent stream as riffles became susceptible to drying.

Although the net effects of invertebrate loss, accumulation and redistribution across different microhabitats and biotope patches appeared limited, they were detectable at the reach scale for all low-flow disturbed reaches. Without access to more preferred habitat conditions over extended durations at the same disturbance intensities, more significant changes in assemblage composition would seem probable based on the changes in invertebrate patch dynamics observed within this approximately two-month period of experimental disturbance, and evidence from similar studies (e.g. Dewson *et al.* 2007a, b).

7.8.4 Riverscape considerations - flow refuge potential of the biotope mosaic

Invertebrate redistribution responses were highly dependent on the availability of and access to suitable wetted habitat, in terms of the spatial configuration and connectivity of different biotope patches in the riverscape mosaic (Taylor *et al.* 1993; Cooper *et al*. 1997; With *et al.* 1997; Palmer *et al.* 2000) and their individual patch features (Sousa 1984; White and Pickett 1985; Hildrew and Giller 1994; Armitage 1995; Wu and Loucks 1995; With *et al.* 1997; Pringle *et al.* 1998; Palmer *et al.* 2000; Silver *et al.* 2004). As such, they firmly endorsed current theoretical models of river patch dynamics (Section 1.4.6) and flow refugium use (Section 1.4.3). The actual combinations of redistribution mechanisms involved, and hence patch-specific losses or accumulations of invertebrates, were complex. They varied not only in concert with biotope dynamics, but also according to seasonal taxonomic composition (Delucchi 1988) and natural differences in the biotope affiliations and hydraulic tolerances of invertebrate taxa (and hence, their flow sensitivities, as explored in Chapter 8). Additional biological attributes, such as taxon-specific behaviours and other life history adaptations, were also clearly influential (Wiens 1989; Lancaster *et al*. 1990; With *et al.* 1997; Winterbottom *et al*. 1997; Lytle and Poff 2004). Although not assessed, it is speculated that biotic interactions, the potential for which increases at small patch scale and during the flow stability typical of the dry season (McAuliffe 1983, 1984), may have further restricted the distribution and abundance of individuals within otherwise suitable refuges as flows declined.

The nature of pre-defined types of streambed patches as refugia at low flows has received comparatively little attention relative to that at high flows (Lancaster and Belyea 1997). There is evidence supporting the role of flow refugia in facilitating invertebrate persistence during high-flow disturbances in perennial rivers (Lancaster and Hildrew 1993a, b; Hildrew and Giller 1994; Matthaei *et al.* 2000; Lake 2000, 2003). Invertebrates were experimentally demonstrated to accumulate in such refugium patches during high-flow disturbances in Whiteadder Water Stream, Scotland (Lancaster 2000). Further, an increase in the proportion of patches acting as hydraulic refugia for invertebrates with varied small, non-scouring experimental

discharge increases was reported by Imbert and Perry (2000). Microform bed clusters of cobbles within patches of larger substrata represented important flood refugia for benthic invertebrates in 12 New Zealand headwater streams, and were considered to similarly provide refugia under extreme low flows (Biggs *et al*. 1997).

Differences in the natural habitat heterogeneity of individual reaches indisputably influenced the extent to which various patches in the overall biotope mosaic mitigated the effects of and were able to provide refuges to invertebrates from flow disturbance (Ward 1976; Scarsbrook and Townsend 1993; With *et al*. 1997; Lake 2000; see Section 1.4.6), whichever redistribution pathways were used (Davis and Barmuta 1989; Sedell *et al.* 1990; Jorde and Bratrich 1998). For spates, the complex riffle architecture of Mountain River, Tasmania, reduced the immediate disturbance impact on invertebrate densities, although it did not affect recovery over several weeks (Robson 1996). Similarly, in the current study, differences in individual patch structure and hydraulic complexity within and among reaches, and with changing discharge, presented an array of spatial and temporal macro-, meso- or micro-scale refugia (*sensu* Townsend and Hildrew 1994; Townsend *et al*. 1997b; Lancaster and Belyea 1997; Palmer *et al.* 2000) that enabled invertebrates to persist during extremely low flows. While individual invertebrate families and species responded differently to this dynamism and hydraulic diversity of low-flow refuges according to their specific biotope preferences and associated hydraulic tolerance ranges, there were commonalities in responses, as described above.

Plausible mechanisms for the observed redistributions of invertebrates encompassed a range from 'between-habitat refugia' among patches, to smaller-scale 'refugia through changes in habitude' or 'within-habitat refugia' (as defined by Lancaster and Belyea (1997); see a full discussion in Section 1.4.3), with persistence possible for all mechanisms in various circumstances. The last mechanism of refugium use and specifically the 'directed flux between microhabitats' model, which predicts short-term movements of individuals into and out of refugia in response to individual disturbance events, could readily be invoked to explain the localised invertebrate shifts observed. In a study of the invertebrate distribution dynamics with flow-mediated alterations in patch hydraulics over a range of discharges, in Broadstone Stream, England, shifts in microdistributions of benthic macroinvertebrates between microhabitat patches defined as refugia and the remainder of the riverbed were similarly consistent with the directed flux model (Lancaster and Hildrew 1993a). Effectively, Lancaster and Hildrew's (1993a) study mirrored aspects of the present one, but for invertebrate redistribution at high flows. While total invertebrate abundances were similar in 'slow', 'fast' and 'variable' patch types (based on benthic shear stress and velocity; Lancaster and Hildrew 1993b) at low flows, under high fluctuating discharges densities were significantly higher in 'slow' than 'fast' patches, suggesting a shift of individuals into the former flow refugia. As in the present case, there were clear invertebrate associations with patch type and taxon-specific responses to changing discharge, and hence, hydraulic conditions. Orthoclads and other chironomids, for instance, were consistently most abundant in 'slow' patches, irrespective of flow conditions. The inter-patch distribution of small nymphs of a dominant stonefly, *Leuctra nigra*, remained unchanged with discharge fluctuations, with a general preference for 'fast'

patches, while large nymphs of the same species, and *Nemurella pictetii*, though exhibiting the same preference for 'fast' patches at low flows, shifted into 'slow' patch refugia at higher flows. For taxa not showing any marked response, it was acknowledged that the discharges experienced might have been insufficient to elicit a shift in habitat distribution. It might similarly be argued that in the present study, for those taxa for which a distinct change in distribution was not obvious, manipulated flow reductions might not have reached sufficient intensity or areal extent to elicit responses. While in Lancaster and Hildrew's (1993a) study, the possibility existed that shifts in microhabitat use were related to longer-term seasonal assemblage responses, rather than short-term reactions to individual flow events, in this thesis controls accounted for that possibility.

In contrast to the situation at higher flows, when passive invertebrate dispersal reportedly dominates and fine-scale habitat selection within the landscape is liable to occur via repeated rejection of unsuitable patches, at low flows invertebrates are able to move or swim across the river bed selecting suitable habitats and thus, potentially exert more control over the patch type they inhabit (Frid and Townsend 1989; Palmer *et al.* 2000). In this study, the redistribution movements of taxa among biotope patches of varying suitability with extreme low flows suggested active refugium use for certain pathways (e.g. migration from riffles into neighbouring runs). Deteriorating local conditions (e.g. patch isolation or desiccation) might well have impeded active habitat selection, however, obliging taxa to remain in or relocate to unfavourable patches (e.g. crowding of rheophiles in riffles or their relocation to pools). A trial conducted at comparatively low flows, in an experimental field study of invertebrate use of refugia at high flows, showed that *Polycentropus flavomaculatus* larvae tracked flow conditions closely and appeared to select control cages with moderate hydraulic conditions in preference to the very low flows naturally occurring in a Scottish upland stream (Lancaster 2000); the converse response was observed in the higher flow trials. Invertebrate assemblages also responded to alterations in hydraulic patterns (based on different depth-velocity combinations) achieved using a flow-modifying device, under a roughly sixfold discharge reduction from natural in the dry season, in two experimental channels fed by Mill Stream, U.K. (Armitage 1995). Short-term responses were associated with invertebrate hydraulic preferences, with the numbers of taxa lowest in areas of low-velocity or negligible flow, and highest in the zone of fastest flow. Despite changes in invertebrate densities and microhabitat proportions from those pre-disturbance, it was concluded that discharge reduction was unlikely to represent a major disturbance where invertebrates were able to access and utilise refugia. However, as also acknowledged by Armitage and Petts (1992), the extent to which such temporary flow refugia would permit invertebrates to survive very low flows would be limited where adverse conditions were prolonged.

Changes in physical habitat with discharge reduction in this study (Chapter 6) affected the total refugium (wetted biotope) area, characteristics of patch refugia (type, hydraulic suitability and geometry), and their spatial arrangement in the riverscape (e.g. proximity to and influence of neighbouring patches of different types) and over time (Townsend 1989; Downes *et al*. 1993, 1998a; Lancaster and Belyea 1997; Lancaster 2000; Silver *et al*. 2004). Moreover, the degree to which biotope patches and their associated microhabitats

became increasingly inhabitable or unsuitable for invertebrates with flow reduction depended in large part on their original 'starting characteristics' in terms of patch characteristics, as illustrated by the differing biotope transformation sequences among and within patch types with discharge (Section 6.5.1, Figure 6.26). Flow-related changes in the size, number and composition of surrounding habitat patches were recognised as potentially altering the ecological dynamics of a single patch, in a study of the effects of diversion on invertebrates in a perennial Hawaiian stream (McIntosh *et al*. 2002). In contrast, in a study of the influence of mesohabitat character on the family structure of benthic macroinvertebrate assemblages in six French streams, a measure of patch diversity that reflected the hydraulic character of the mosaic of neighbouring patches exerted little influence on the invertebrate composition of a sampled patch (Beisal *et al.* 1998).

Larval chironomids actively responded to habitat patch type and spatial arrangement in Goose Creek, U.S.A., based on quantified dynamics in a wide array of patch metrics (e.g. size, shape, perimeter to area or P: A ratio, degree of contagion, downstream distance between patches) for different riverscape patch types at multiple sites (Palmer *et al.* 2000). Models that included spatially-explicit data on patch arrangements and characteristics were more powerful predictors of the variation in landscape-level abundances of invertebrates than those based solely on non-spatial descriptors, including flow (e.g. magnitude of last flood). Faunal persistence increased when refugia patches were small and 'soft-edged' - that is, surrounded by a habitat matrix delimited by comparatively small-scale differences in hydraulics, which was potentially habitable during disturbance-free periods (Lancaster and Belyea 1997; Lancaster 2000). Lancaster (2000) further suggested though, that a mix of patch sizes might be important for invertebrate retention and persistence, with large refugia (such as the runs in this study) potentially more stable than small ones. With experimental flood disturbance in Goose Creek, streambed patch stability interacted with patch arrangement such that disturbances that maintain fragmented patch landscapes (i.e. small patches and high P: A ratios) were shown to be potentially more influential in invertebrate persistence and retention than aggregated landscapes (i.e. higher mean areas, but lower patch numbers, perimeters and P: A ratios), by supporting higher chironomid densities (Silver *et al*. 2004).

While not an explicit focus of this chapter (but explored in Section 8.6), the extent of influence of changes in select patch metrics on invertebrate responses at unnaturally low flows, as wetted area became fragmented and patch characteristics altered, is acknowledged as an important consideration requiring investigation. Certainly, there seemed to be differences in the natural 'softness' of patches among the experimental rivers, due to a combination of high spatial habitat heterogeneity and associated hydraulic variability at small patch scales, enhancing their potential accessibility and efficacy as low flow refugia. In this context, natural patchiness and availability of refugia was high for all of the rivers, but particularly so in the Riviersonderend reach, an upper mountain stream with a naturally variable low flow regime, and where biotopes were often small and relatively weakly hydraulically delineated. The natural degree of 'internal biological cohesion' of these biotopes was correspondingly weakest for this river as well. Palmer *et al.* (1991) in encountering a similar situation in the upper Buffalo River, when compared with lower river zones, highlighted the potential

with a variable flow pattern for rapid and more frequent changes in patch physical character over small scales. High mesoscale patch heterogeneity provides for a wide range of hydraulic conditions, enabling invertebrates to locate adjacent suitable habitats at hydraulic optima outside of average conditions (Jowett and Richardson 1990; Wood and Petts 1994; Townsend and Hildrew 1994; Armitage 1995; Beisal *et al.* 1998; Boulton 2003), so that they are less susceptible to temporal variations in discharge than the benthos of more homogeneous environments. Wood and Petts (1999) maintained, for instance, that the persistence of hydraulic habitat diversity throughout a drought in a U.K. chalk stream, even with severely reduced mean velocities, prevented the elimination of most invertebrate taxa and facilitated their rapid recovery from hydraulic refugia once normal flows resumed. Plausibly then, various flow-mediated patch characteristics might have had a central contributing role in the limited responses of invertebrates to low-flow stress in the current study (see also Section 6.7.3). They might have ameliorated the more pronounced barriers to invertebrate redistribution and refuge access under artificial low flows, as biotopes transformed into more hydraulically discrete entities within the unnaturally highly fragmented riverscape, and critical habitat thresholds for invertebrates were potentially exceeded (Chapter 8).

8. CHARACTERIZATION OF ECOLOGICALLY RELEVANT LOW FLOWS: RELATING INVERTEBRATE RESPONSE TO ABIOTIC MEASURES OF FLOW DISTURBANCE

8.1 INTRODUCTION

Multiple factors directly or indirectly influence benthic macroinvertebrate response to low-flow disturbance, from hydrological regime and physical habitat conditions, through to life history attributes and biotic interactions (Section 7.1). There are several main ways in which these contributing abiotic, and less commonly, biotic factors have been explicitly linked to invertebrate responses to low flows, particularly but not exclusively for purposes of river flow management. A longstanding approach, though not commonly applied from a flow disturbance perspective, has focused on defining mesohabitat-invertebrate associations and, in fewer instances, their dynamics with flow or flow-related factors (Tharme 1996, 2003; Newson and Newson 2000). More typically, hydraulic microhabitat and its suitability for invertebrates have been at the forefront of attempts to establish relevant low flow patterns and ecological flow requirements for taxa (Gore 1978, 1987; 1989, 1998; Gore and Judy 1981; Orth and Maughan 1983; Orth 1987; Gore and Nestler 1988; Jowett and Richardson 1990; Jowett *et al*. 1991; Jowett 1997, 2003). Finally, in recent years, ecologically relevant flow statistics and their relationships with various measures of invertebrate community structure and function have gained prominence in characterizing ecologically meaningful flows, in pace with the exponential growth of ecohydrology as an applied discipline (Tharme 2003; Arthington *et al.* 2006; Poff *et al.* 2010; Section 1.4 and Chapter 9). There has been a shift away from the previously popular use of single low flow indices to represent invertebrate flow needs as minimum flows (Tharme 1996, 2003; Pyrce 2004; Sections 1.5 and 4.1.2) towards more comprehensive assessment of the connections between flow disturbance regime and invertebrate response. This has been principally driven by a demand for such information to fuel holistic environmental flow determinations (Section 1.5.6).

8.1.1 Mesohabitat-invertebrate assemblage associations and low flow dynamics

Research on the associations between various types of mesohabitats and invertebrate assemblages is not novel. Even early on in river ecology (Stehr and Branson 1938; Edington 1965; Chutter 1969; Hynes 1970; Ward 1976) the structure of a 'habitat' (and the different hydraulic conditions it integrates) was recognised as determining the faunal structure of the associated community, with variously discrete assemblages occupying different habitat types (Barmuta 1989; Wadeson 1996). For instance, in the 1930s in Rock Riffle stream, U.S.A, it was shown that while some invertebrate taxa were ubiquitous, there were assemblages characteristic of different biotopes (Stehr and Branson 1938). Numerous published studies have since

accumulated that lend credence to that understanding, not only for invertebrates (Sheldon and Haick 1981; Logan and Brooker 1983; Gurtz and Wallace 1984; Pridmore and Roper 1985; Barmuta 1989; Palmer *et al.* 1991; Boulton and Lake 1992a; Scarsbrook and Townsend 1993; Armitage *et al*. 1995; Wohl *et al.* 1995; Pardo and Armitage 1997; Beisal *et al.* 1998; Tharme and King 1998; Kay *et al*. 1999; Wood *et al*. 1999; Tickner *et al.* 2000; Choy *et al.* 2000; Buffagni 2001; Brunke *et al.* 2001), but also for fish assemblages (e.g. Leonard and Orth 1988; Aadland 1993; Lamouroux and Souchon 2002).

While considerable effort has been expended on describing the nature of associations of invertebrate assemblages, and component taxa, with specific types of spatially defined mesohabitats (physical or hydraulic biotopes, functional habitats, etc.; Section 1.4.8), disproportionately less attention has been given to assessing how such habitat units change ecologically in their availability or suitability under different temporal flow regimes, especially at extremely low flows. Armitage *et al*. (1995, p. 384) commented on the lack of such "prediction of the effects of disturbance on the availability of instream habitat types" as a deficiency in connecting existing mesohabitat or similarly based assessments of stream condition with readily accessible information on lotic response to disturbance in general. Moreover, often the responses of invertebrates to altered flows have simply been assumed, with the physical dynamics of mesohabitat patches with flow regime the primary focus (see Chapter 6). In other instances, while the associations of particular groups of invertebrates with mesohabitats have been clearly demonstrated, the connections to the underlying flow-related hydraulic (or other abiotic) factors supporting such associations, or directly to flow regime characteristics have not been investigated. Seldom therefore, have the potential changes in the characteristics of such invertebrate-mesohabitat associations with biotic response to low flow (or even flood) disturbance been used as a means to identify ecologically meaningful flow events, as attempted in this thesis. As Armitage and Pardo (1995) and Brunke *et al.* (2001, p. 672) advocated "As the fauna of different mesohabitats might be affected differentially from a reduction in flow, the effects of water abstractions on invertebrates have to be evaluated on the scale of mesohabitats", to address not only the flow requirements of individual taxa, but also more broadly to protect mesohabitat diversity.

The nature of associations of invertebrates with different mesohabitat types

The potential utility of delimiting a range of habitat patch descriptors and exploring their links with discharge, hydraulics and water chemistry for river management was recognised, but not explored, in a mesohabitat study in a small English chalk stream, Wool Stream (Tickner *et al.* 2000). Differences in invertebrate community composition, more consistent and pronounced than those among reaches, were described for seven dominant vegetated (e.g. 'emergent vegetation', '*Ranunculus*') and mineral (e.g. 'sand', 'pebbles/gravel') mesohabitats, the mapped distributions of which varied among reaches. Information on the distributions of mesohabitat types and assemblages inhabiting them was shown to be useful as the basis of an index of stream quality (the Mesohabitat Quality Score) which incorporated faunal richness and a relative measure of taxon preference for individual mesohabitats. In six French streams, mesohabitats were defined based on various combinations of hydraulics, with mesospatial heterogeneity optimum at moderately high

velocities and/or turbulence, coupled with shallow waters (Beisal *et al.* 1998). Velocity particularly, and water depth, were secondary only to substratum as major determinants of benthic invertebrate structure and diversity at family-level across the mesohabitats. A strong relationship also existed between assemblage structure and mesohabitat spatial variability. Pool, riffle, transition and bedrock functional habitats were differentiated based on differences in their invertebrate composition and abundance in an Italian river (Buffagni 2001). For instance, overall abundances and those of specific taxa (e.g. *Baetis alpinus*, *Rhithrogena* spp., *Ecdyonurus helveticus*) were greatest for riffles, while other taxa were most abundant in pools (e.g. *Habroleptoides* sp., *Leuctra* sp.). Distinct and consistent differences in invertebrate assemblage composition were attributed to differences in the physical character of depositional, cobble-riffle and bedrock outcrop habitat types, each with differing hydraulic characteristics, in the U.S. Nantahala Basin (Wohl *et al.* 1995). Cobble riffles were typified by highly diverse assemblages, and fast-flowing bedrock patches by mayflies, stoneflies and net-spinning caddisflies. Dipterans, odonates and trichopterans, in contrast, characterized depositional habitats. In a study of multiple sites on northwestern Australian rivers, there were significant differences in taxon richness across different habitats, with most habitats exhibiting a distinctive faunal composition (Kay *et al*. 1999). Certain taxa were largely confined to particular habitats with, for example, simuliids, hydropsychids and helicopsychids strongly associated with riffles. Differences in family-level assemblage composition were apparent for four habitats in the Brisbane River, Australia, with riffle and pool faunas diverging most and in relation to velocity gradients (Choy *et al.* 2000). Riffles included high numbers of families (and abundances) associated with high velocities (e.g. Simuliidae, Hydropsychidae, Elmidae), while pools harboured several taxa favouring slow-flowing areas. Multiple, principally upland, rivers of the U.K. and North America showed various strengths of association among macroinvertebrate assemblages, and riffles and pools, with the specific families and species characteristic of each habitat varying across rivers (Logan and Brooker 1983).

In a first biological validation of mesoscale physical biotopes (Section 1.4.8 and Chapter 6) in the U.K., using seasonal assemblages from nine of Padmore's (1997) least-impacted sites, site species assemblages were separated in ordination space primarily by water quality variables (i.e. temperature, pH, conductivity, EC) that reflected the upland to lowland continuum, with hydraulic variables describing biotope character, principally Froude number (Fr), influential only at a secondary level (Grundy 1996, cited in Newson and Newson 2000). Palmer *et al.* (1991) found specific species assemblage associations with eight visually defined 'erosional' (visible flow turbulence, e.g. riffles) and 'depositional' (areas of zero-velocity water, e.g. stony backwaters, marginal vegetation out of current) biotopes in the upper, middle and lower reaches of the South African Buffalo River. The nature of the assemblages varied across biotope types with many taxa showing distinct preferences among multiple biotopes, but no singular biotope specificity. Biotope specificity also varied among reaches. Similarly, different assemblages were associated with hydraulic biotopes at sites along the perennial Western Cape Olifants River (Tharme and King 1998). In an effective approach, building from taxon-hydraulics relationships (Section 8.1.2) up to the mesohabitat scale, invertebrate species-specific relationships between Fr and abundances were used to reflect different

invertebrate-biotope associations (Jowett 1993). Across pools, runs and riffles, for example, *Aoteapsyche* spp. were most abundant in riffles and *Pycnocentrodes* spp. in runs. *Coloburiscus humeralis* was equally abundant in both riffles and runs, and *Olinga feredayi* showed no biotope preference.

Although the majority of such studies have supported the association of various invertebrate assemblages and individual taxa with a range of different mesohabitat types, associations are not always distinct. Barmuta (1989, p. 225, Table 1) visually distinguished eight habitats in the Australian Acheron River, using quantified hydraulic attributes of flow type, velocity, water depth and substratum character, but acknowledged that types partially overlapped. Consequently, rather than distinct associations between species assemblages and the hydraulic habitats, which ranged from 'riffles', through slow runs/pools, to 'exposed pebbles', a gradual transition occurred in assemblage structure between erosional and depositional extremes. Although the primary division was into an erosional habitat group, with higher abundances of rheophilous taxa, and a depositional group, that lacked rheophilic taxa and included species intolerant of flow turbulence, most of the faunal complement of the latter group were capable of persisting in erosional habitats; few taxa showed unique preferences for depositional patches. Barmuta (1989) identified a need for more precise descriptions of near-bed hydraulics to better elucidate finer-scale differences in assemblage structure and sufficiently differentiate taxon-habitat associations. Continuous rather than discrete changes in invertebrate associations with physical habitat were also found in Grant Creek, U.S.A., with velocity, organic detritus and substratum composition most influential (Sheldon and Haick 1981). Hydraulic habitat differentiation was observed, however, among stonefly, trichopteran and mayfly species in relation to their known hydraulic preferences. Although invertebrate assemblage composition did not differ significantly between riffle and pool habitats in Timber Creek and Kyeburne Stream, New Zealand, the habitats could be characterized according to differences in functional feeding groups (Scarsbrook and Townsend 1993).

Eleven mesohabitats representing discrete, seasonally distinct faunal units (e.g. '*Ranunculus* fast', 'gravel slow') were identified in Mill Stream, a managed side-channel of the English River Frome (Armitage *et al*. 1995; Pardo and Armitage 1997). Complementary mesohabitat hydraulic characterization revealed a first separation on the basis of substratum type, followed by velocity and then, less strongly, depth and discharge (Pardo and Armitage 1997). Invertebrate assemblage composition reflected a gradual transition in relation to these hydraulic factors, with general patterns the same for families and species. Differences were recorded among mesohabitats in relative family-level richness, abundance, dominance and other biotic indices, as well as their variability, with indicator species identified (Armitage *et al*. 1995). Streamflow regulation effects were reflected in altered mesohabitat representation, with higher proportions of mesohabitats associated with deep, slow-flowing conditions in the regulated than the unimpacted reach (Armitage and Pardo 1995). These spatial changes were of greater importance than seasonal trends, leading Armitage and Pardo (1995) to recommend a (meso) habitat-based approach to flow regulation above assessments based solely on benthic community change. Across the modified Mill Stream, Little Stour River and River Gadder, mesohabitat diversity patterns were similar, for three mesohabitats identified primarily on substratum type (Wood *et al*.

1999). Mesohabitat-species associations were also consistent across the rivers, with particular species indicative of each mesohabitat type and species-environment variation among mesohabitats driven principally by significant differences in hydraulics. Although Wood *et al*. (1999) went on to explore the impacts of different degrees of low-flow stress on overall assemblage composition across the rivers, related changes in taxon-mesohabitat associations were not a focus.

Outside of such general mesohabitat-assemblage based approaches, instances where mesohabitats have been physically described, mesohabitat-invertebrate associations identified and related with habitat hydraulics, and the resultant relationships used to characterize ecologically relevant low flows appear scarce. In one example, with variously distinct invertebrate assemblages inhabiting eight hydraulically different mesohabitats in the River Spree, Germany, mesohabitat-specific relationships between velocity and discharge, in combination with species-specific velocity tolerances and optima, were used to assess the impacts of flow reduction on invertebrates and hence, to elucidate minimum flow requirements (Brunke *et al.* 2001); taxa were classified with regards flow preference into seven categories. Invertebrate responses to velocity, and hence corresponding discharges, highlighted several significant relationships between the presence/absence of rheophilic species (assumed most liable to be impacted by flow reduction) and discharge magnitude. Clear associations between mesohabitats, their hydraulic character and within-reach diversity, and invertebrate taxa of differing natural hydraulic and flow sensitivities, were also identified for multiple sites on the River Glen, U.K. (Bickerton 1995). Relationships between invertebrate communities and low-flow disturbance history were then described for this hydrologically altered river (Section 8.1.3).

8.1.2 Relationships between invertebrates and hydraulic indices at low flows

The most concerted efforts, and some of the earliest, to characterize ecologically relevant low flows for invertebrates have been underpinned by and stimulated to evolve through the science of ecohydraulics (introduced in Section 1.4.8). Studies of the specific microhabitat distributions of invertebrates within biotopes started early in the late 1950s, though acknowledgement of ecohydraulics as a discipline connected with ecohydrology was recent.

Many invertebrate taxa demonstrate specific preferences and varying, sometimes narrow, limits of tolerance for different hydraulic conditions (Gore 1977; Gore 1978; Bovee *et al.* 1978; Gore 1987), based on the interplay of which they select their habitats (Ulfstrand 1967; Section 8.1.1). Consequently, they will be affected by changes in flow pattern (Brittain and Saltveit 1989; Jowett *et al.* 1991). Statzner *et al*. (1988, p. 321) in investigating the influence of flow on taxa felt that "the hydraulic environment should be expected to have a major impact on distribution patterns of lotic macroinvertebrates". They also argued for a more complete description of reach physical conditions that encompassed "frequency distributions of complex hydraulic key characteristics at various discharges" to increase prediction and replication in lotic studies, particularly as relatively large discharge fluctuations alone did not necessarily result in significant changes in complex hydraulic characteristics (Statzner *et al*. 1988, p. 343). The understanding that hydraulic factors,

rather than discharge *per se*, may be of greater immediate significance in influencing invertebrate responses to flow disturbance (Armitage 1995; Petts *et al*. 1995; Brunke *et al.* 2001) has fuelled an expansive body of work on invertebrate-hydraulics relations (as well as on various species' adaptations to flow hydraulics).

A veritable plethora of studies have focused on the influence of various combinations of hydraulic factors on invertebrate assemblage composition and taxon distributions, among others: Ambühl (1959, cited in Hildrew and Giller 1994); Edington (1965, 1968); Ulfstrand (1967); Chutter (1969); Cummins and Lauff (1969); Hynes (1970); Ward (1976a); Minshall and Minshall (1977); Williams (1980); Statzner (1981a, b); Gore and Judy (1981); Alstad (1982); Statzner and Holm (1982); Orth and Maughan (1983); Ciborowski (1983); Minshall (1984); Resh and Rosenberg (1984); Nowell and Jumars (1984); Statzner and Higler (1986); Chance and Craig (1986); Statzner *et al*. (1988); Gore (1989); Davis and Barmuta (1989); Armitage and Petts (1992); Campbell (1992); Death and Winterbourn (1994, 1995); Hart *et al.* (1996); Choy (1998); Hart and Finelli (1999); and Jowett (2003). Studies have gone further, exploring how the availability and suitability of hydraulic habitat for invertebrates alter with flow induced environmental change, from the reach scale to the finest grain of microhabitat, often in relation to assessing environmental flows (Section 1.5.5). Surprisingly, in few such cases have changes in the actual dynamic of the relationship between hydraulic descriptors and taxa with changing flows been acknowledged or evaluated as potentially indicative of a flow-disturbance response, as done in this thesis.

Emphasis has been placed on invertebrate response, particularly in terms of taxon densities, to standard or 'core' (Chapter 6) hydraulic habitat variables, more complex ('derived') ones describing both micro- and macro-flow conditions (Statzner *et al.*1988; Davis and Barmuta 1989; Gordon *et al.* 1992; Wadeson and Rowntree 1998; Vadas and Orth 1998), or some combination (Sections 1.4.8 and 3.4.3). While for benthic invertebrates, near-bed hydraulic conditions are probably of more direct influence than variables that describe the macro-flow environment (Davis and Barmuta 1989; Jorde and Bratrich 1998; Jowett 2003), several of the existing diversity of variables not directly related to the immediate environment experienced by the benthos (e.g. mean-column velocity, Fr) have still correlated well with invertebrate distributions. Moreover, several of them have been shown to have considerable merit in flow-related characterization of habitat conditions at the mesohabitat patch scale (Kemp *et al*. 2000; Chapter 6) and in ascertaining the potential ecological significance of such patches for biota (Chapter 7 and below). They also include several of the hydraulic habitat descriptors typically used in environmental flow assessments (O'Keeffe *et al*. 2002).

Relationships between patterns in invertebrate density and other aspects of composition, and hydraulics typically result from the intricate interplay of multiple hydraulic factors, many highly intercorrelated (Quinn and Hickey 1994; Jowett 2003), rather than simply individual variables (Minshall 1984). Consequently, relationships between hydraulic variables and invertebrate habitat preferences at various discharges have been posited to be complex and therefore, debatably, best reflected by derived hydraulic indices (Statzner and Holm 1982; Statzner 1988; Statzner *et al*. 1988; Davis and Barmuta 1989). Such indices constitute one

suite which considers the microenvironment in which many species reside (e.g. shear velocity (v_*), roughness Reynolds number (Re_*), shear stress) and a second set that integrates conditions in the entire water column (e.g. Reynolds number, Re, Fr) (Statzner *et al.*1988; Davis and Barmuta 1989; Gordon *et al.* 1992; Wadeson and Rowntree 1998). Complex indices or combinations of hydraulic variables have been shown to be capable of explaining a greater proportion of variation than single variables, though not in all instances (Jowett *et al.* 1991; Quinn and Hickey 1994). According to Jowett (2003), field studies have been unable to demonstrate that complex indices are necessarily better predictors of benthic invertebrate abundances and habitat hydraulic requirements than suitability functions that consider basic hydraulic variables independently (Jowett *et al.* 1991; Quinn and Hickey 1994; Gore 1998; this study).

Relationships between invertebrates and hydraulic variables are usually taxon-specific (Minshall 1984; see below). Certain taxa are recognised as 'obligate' or 'sensitive' rheophiles, unable to survive in standing water, eliminated almost immediately with loss of flowing current, and/or dependent on flowing water conditions for lifecycle completion (Campbell 1991, 1992; Fonseca and Hart 1996; Growns and Growns 2001; O'Keeffe *et al*. 2002; Boulton 2003). Precise microhabitat selection in high-velocity areas, interspecific partitioning of space, and individual behavioural positioning in relation to hydraulics have been especially well documented in taxa that utilise the current for active feeding (e.g. filter-feeding simuliids, net-spinning trichopterans, some chironomids) or to meet respiratory demands (e.g. leptophlebiid spp.) (Edington 1965, 1968; Ward 1976; Alstad 1982; Chance and Craig 1986; Jowett *et al*. 1991; Campbell 1992; Fonseca and Hart 1996; Hart *et al.* 1996; O'Keeffe and Dickens 2000). Conversely, detritivores, for instance, select areas of low velocity and Re for feeding (Quinn and Hickey 1994). Many species whilst preferring flowing water conditions may be facultative rheophiles, or euryoecious and able to survive the disappearance of preferred habitats for extended periods (Davies *et al*. 1994; O'Keeffe *et al*. 2002). Although typically assumed to be the case, the flow-related hydraulic preferences, and hence microdistribution patterns, of benthic invertebrates are not necessarily uniform throughout their life cycles or in relation to differences in size (Hynes 1970; Gore 1983; Jowett and Richardson 1990). Often overlooked, and yet vital in the context of low-flow disturbance, is that temporal changes in the habitat requirements of macroinvertebrates should be factored into assessments of the hydraulic habitat preferences of invertebrates, if prediction of flow needs or responses are to be accurate (Gore 1983). Gore (1989) used the crayfish, *Orconectes neglectus*, as an example, as it exhibits size-related flow and substratum preferences and, in addition, dimorphic velocity preferences during that part of the year when females carrying eggs migrate to riffles.

Invertebrate responses to hydraulic indices and their alteration with discharge

Selection of variables to describe species-habitat associations is rendered difficult by the differences that can be expected in the relative importance of various hydraulic variables to individual species (Aadland 1993). Of the core measures of hydraulic habitat known to respond to changing flows (Chapter 6), however, current velocity has shown itself a major factor, if not the best single predictive variable, correlating with the

distributions and abundances of a wide range of taxa (Ambühl 1959, cited in Hildrew and Giller 1994; Ulfstrand 1967; Chutter 1969; Ciborowski 1983; Jowett *et al*. 1991; Campbell 1991, 1992; Jowett 2003; Lancaster and Belyea 2006; e.g. Statzner *et al*. 1988, p. 310, Table 1). Invertebrates may respond differently to near-streambed velocity, depending on substratum and depth conditions with which there are intimate interrelations that make it difficult to fully separate individual effects (Minshall 1984; Mathur *et al*. 1985; Statzner *et al*. 1988; Davis and Barmuta 1989; Jowett *et al*. 1991). Less well studied are relationships of invertebrates with water depth (Campbell 1991, 1992). Mean velocity and complex hydraulic variables are considered to be more useful than substratum character in describing the distributions of lotic invertebrates, with the last deemed a poor descriptor of near-bottom hydraulics (Statzner *et al*. 1988). Varying, sometimes strong preferences of different invertebrates for substratum type, however, have been observed (e.g. Orth and Maughan 1983; Minshall 1984; Jowett *et al*. 1991; King and Tharme 1994).

Froude number, as a multi-scale index of near-surface and free-flow turbulence, has been the most commonly adopted derived hydraulic index (Statzner *et al*. 1988). It has shown strong relationships directly with invertebrate abundances and distribution patterns (Gore 1978; Statzner 1981a, b; Orth and Maughan 1983; Wetmore *et al.* 1990; Jowett *et al.* 1991; Davis and Growns 1991; Quinn and Hickey 1994; Jowett 1993; Gore 1996; Section 3.4), as well as with different mesohabitat types (Wadeson 1996; Padmore 1997, 1998; Vadas and Orth 1998; Kemp *et al*. 2000; King and Schael 2001; Chapter 6). The variable flow directions associated with turbulence and its important influence on instream processes also make other turbulence indices central in taxon distributions (Statzner 1981a; Statzner and Holm 1982; Robson *et al*. 1999; Jowett 2003). Several additional complex variables, including those reflecting near-bed flow conditions, have been shown to affect invertebrate responses to flows (Bovee *et al*. 1978; Statzner 1981b; Statzner *et al*. 1988; Quinn and Hickey 1994; Gore 1996; Jorde and Bratrich 1998). At an even finer scale, invertebrate taxa have shown various correlations with flow microhydraulics linked to the spatial heterogeneity of stone microenvironments (Boulton *et al.* 1988; Davis and Growns 1991; Bouckaert and Davis 1998).

The complexity of river microflow regimes suggests that suitable microhabitats for invertebrates are able to extend over a range of hydraulic conditions with which the biota can cope (Jowett 2003). Moreover, differences in invertebrate hydraulic preferences and tolerances are likely influenced by the range of hydraulic conditions available among different rivers. Regardless of the specific mesohabitats they inhabit, the hydraulic preferences of many taxa are typically directly used to identify hydraulic optima and ranges of tolerance to various natural or, less commonly, altered discharges. Taxa with naturally narrow hydraulic tolerances potentially serve as particularly suitable indicators (Stalnaker and Arnette 1976). Individual and more generic relationships between invertebrates and single or multiple hydraulic variables have been demonstrated for a diverse range of taxa (as well as for target functional feeding groups, maximal community diversity, etc.) in different rivers (Gore 1977, 1978, 1987, 1989, 1998; Bovee *et al.* 1978; Gore and Judy 1981; Statzner 1981b; Orth and Maughan 1983; Morin *et al*. 1986; Statzner and Higler 1986; Orth

1987; Gore and Nestler 1988; Jowett and Richardson 1990; Jowett *et al.* 1991; King and Tharme 1994; Quinn and Hickey 1994; Jorde and Bratrich 1998; Paxton 2000; Brunke *et al.* 2001; Gore *et al.* 2001; Jowett 2003). Illustrative examples are given below and in Section 8.8.2. Characteristically, the hydraulics-invertebrate response relationships are generated in the form of habitat suitability index (HSI) curves, reflecting hydraulic habitat availability, utilisation and/or preference under various discharges (Bovee 1986; Slauson 1988).

For instance, Gore and Judy (1981) derived habitat preference curves based on velocity, depth and substratum for 19 different invertebrate taxa. An exponential polynomial HSI model, which incorporated a velocity-depth interactive factor, successfully predicted larval densities of four simuliid species (Morin *et al*. 1986), while in another case a significant relationship was established between simuliid density and viscous sub-layer thickness (Statzner 1981b). Simple and complex hydraulic characteristics were also used to examine the hydraulic habitat preferences of the water bug, *Aphelocheirus aestivalis* (Statzner *et al*. 1988). Seasonal correlations between the abundances and sizes of several species and microhabitat conditions, described using both a dimensionless index of 'hydraulic stress' dependent on water depth, velocity and channel roughness, as well as an index reflecting laminar sub-layer thickness, were found in the German Schierenseebrooks (Statzner 1981a). *Hydropsyche* spp., for example, showed increases in abundances with increasing hydraulic stress. Various significant positive or negative relationships, and of different forms, were found between ten major riffle species and one or more of depth, velocity, substratum type and Fr, individually or expressed as joint hydraulic preference factors, in Glover Creek, U.S.A. (Orth and Maughan 1983). Mean hydraulic conditions were identified at which riffle diversity, numbers of taxa, and biomass and abundance were maximised. The majority of 12 common taxa across four New Zealand gravel-bed streams of differing size and flow regime showed significant hydraulic habitat preferences that were usually consistent among rivers (Jowett *et al*. 1991; Quinn and Hickey 1994). Some taxa showed narrow tolerance ranges indicating high flow-hydraulics specificity, while others, such as the dominant leptophlebiid, *Deleatidium*, exhibited the broad hydraulic tolerances indicative of habitat generalists (Jowett and Richardson 1990; Jowett *et al*. 1991; Jowett 2003). Differences in hydraulic habitat preferences were even apparent for seven large taxonomic groupings in the Waingawa River, N.Z. (Jowett and Richardson 1990). Most groups showed significant preferences for at least two of the variables depth, velocity and substratum, where each variable was considered independently. The 'other mayflies' and 'cased caddisflies' groups inhabited shallow, lower-velocity waters, for example, whereas Diptera preferred high velocities and was the only group selecting for deep areas.

Generalised habitat preferences and associated depth and velocity ranges have also been established for some groups of taxa and rivers. Generic preference curves were developed, for example, for Ephemeroptera, Plecoptera and Trichoptera in U.S. streams (Gore *et al.* 2001). In a group of N.Z. rivers, generalised HSI curves were developed for *Deleatidium*, and for the Waingawa R. they constituted part of a River Hydraulics and Habitat Simulation Program (RHYHABSIM) application to determine invertebrate flow-related

requirements (Jowett and Richardson 1990; Jowett *et al*. 1991). Across numerous N.Z. river locations representing a wide range of flow regimes and hydraulic habitats, river size-related hydraulic preferences were apparent, although a few taxa exhibited consistent hydraulic tolerances across different rivers (Jowett 2003). Factors other than hydraulics obviously also influence local species distributions and abundances in these various instances (Bovee 1982; Orth 1987; Jowett and Richardson 1990; Lancaster and Belyea 2006). For example, only 25% of the variation in *Deleatidium* abundances in the Waingawa R. could be explained by depth, velocity and substratum, with the additional inclusion of periphyton biomass resulting in the best-fit model overall (Jowett and Richardson 1990).

Linking invertebrate tolerances and riverscape hydraulic habitat to flow dynamics

Despite the attention given invertebrate relationships with discharge-mediated hydraulics, a less concerted effort has been made to connect them with the reach spatial dimensions of hydraulic habitat, particularly at mesohabitat scale at different flows, and for predictive purposes. In an early landscape-focused approach though, the microdistributions of Ephemeroptera, Plecoptera, Trichoptera and Simuliidae were examined in relation to three-factor association grids of water depth, velocity and substratum categories, mapped at two seasonally different discharges in Lapland streams (Ulfstrand 1967). Distinct preferences and associated varying bands of tolerance for individual hydraulic variables were demonstrated among species based on their distribution patterns, with some taxa more actively avoiding certain hydraulic conditions than others and seasonal microdistribution differences apparent. The preferred hydraulic habitat of a filter-feeding caddisfly, *Brachycentrus occidentalis*, in Wilson Creek, U.S.A., was similarly characterized by mapping flow-related conditions for depth, velocity, Fr and water surface slope, in relation to the streambed distribution of larvae (Wetmore *et al*. 1990). Near-bed velocity was an important determinant of patch-scale riffle densities of Baetidae, Heptageniidae and leuctrid plecopterans in a Scottish stream, Faseny Water, using both models describing central tendencies, and maximum and minimum limits of response (Lancaster and Belyea 2006). Scatter in invertebrate abundance-hydraulics relationships was attributed to multiple factors operating at a range of scales, from inter-individual variation, to biotic processes and alterative environmental gradients within and beyond the individual patch.

Consistently strong associations were found between the ambient flow environment described by hydraulic gradients at various discharges, and patterns of invertebrate community distribution in the Canadian Fraser River (Rempel *et al.* 2000). Some 52% of total variation was explained by a primary hydraulic gradient comprising a diverse suite of variables (near-bed shear velocity, boundary Reynolds number, mean velocity, Fr, turbulence intensity, Re) that corresponded positively with increasing water depth. Invertebrate taxa were strongly associated with reach hydraulic conditions, with densities highest in shallow locations of lowest hydraulic stress. An attempt at invertebrate classification according to the flow exposure groups of Growns and Davis (1994, cited in Rempel *et al.* 2000) was not considered particularly useful. Distributions in relation to hydraulic gradients were taxon specific, with different species exhibiting positive or negative correlations with individual descriptors. Family responses were also clearly associated with hydraulic

preferences with experimentally induced shifts in five different depth-velocity zones under discharge reduction (six-fold and during the dry season) in two experimental channels of Mill Stream, U.K. (Armitage 1995).

Identifying flow needs based on invertebrate responses to discharge-altered habitat hydraulics

An explicit link between the hydraulic tolerances of benthic invertebrates and physical habitat dynamics with discharge has oftentimes constituted the basis for characterizing ecologically meaningful flows (Gore and Nestler 1988; King and Tharme 1994; Tharme 1996; Gore 1998; Growns 1998). The expectation implicit in environmental flow methodologies reliant on flow-habitat modeling, such as the Instream Flow Incremental Methodology and holistic approaches (Section 1.5), is that changes in instream hydraulic habitat with discharge will lead to invertebrate responses in the form of changes in species abundances and distribution patterns (Jowett *et al*. 1991). The majority of such cases have involved the use of the kinds of hydraulic suitability relationships described above to identify invertebrate flow requirements. Most often, characterization of ecologically relevant flows has relied on conventional habitat modelling where a hydraulic model is linked to the preference curves for various taxa, to estimate changes to the habitat available to them with changing discharge (Milhous *et al*. 1989; Lamouroux and Souchon 2002; Tharme 2003). Invertebrate responses to the flow-related changes in habitat availability and quality tend to be based on characteristic responses to natural flows, which may be assumed rather than demonstrated. Seldom have HSI curves been used as a tool specifically to identify shifts in the hydraulic associations or preferences of invertebrates in relation to low-flow disturbance, as done in this thesis, although some known examples are outlined here.

In an early example of the use of habitat suitability-invertebrate relations to characterize ecologically meaningful flows, hydraulic response surfaces were used to identify adequate instream flow conditions for benthos in the Tongue River, U.S.A. (Bovee *et al*. 1978). In this case, the relationships were validated when dramatic flow reduction resulted in increased drift, particularly of the indicator *Rhithrogena*, at a discharge where hydraulic simulations predicted few individuals or complete absence of suitable depth-velocity combinations for this species (Bovee 1982, cited in Gore 1989). As part of the determination of an ecologically acceptable flow regime for the English River Babingley, Physical Habitat Simulation program (PHABSIM) habitat-flow time series were generated that encompassed a drought period, for six indicator invertebrates for which relationships between naturalised flow percentiles and hydraulic habitat suitability were compared and benchmark flow thresholds identified (Petts *et al*. 1999). The effects of different flow regimes, including minimum flows, on hydraulic habitat availability for three invertebrate species for which preferences for bottom shear stress were determined, were simulated for the Kocher River, Germany, using the Computer Aided Simulation Model for Instream Flow Requirements in regulated streams (CASIMIR; Jorde 1996; Jorde and Bratrich 1998; Section 1.5). A near-bottom velocity (NBV) preference curve for *Hydropsyche instabilis* was used to successfully predict its response to velocity changes with experimental

discharge alteration in Perlbach Stream (Statzner *et al*. 1990). In the same German stream, derived relationships between an index of near-bed hydraulics and discharge, along with species preference curves developed for similar streams elsewhere for *Dinocras cephalotes*, *Baetis rhodani*, and *Gammarus fossarum* were also used to predict population decreases with discharge reductions.

8.1.3 Characterization of ecologically relevant flows based on hydrological indices and complementary abiotic descriptors of disturbance

Attempts to characterize ecologically relevant flows, through direct links to flow statistics that represent flow regime characteristics or events expected to hold particular relevance for invertebrates, are an increasingly mainstream direction of ecohydrology (e.g. Jowett and Duncan 1990; Clausen and Biggs 1997; Caruso 2002; Monk *et al.* 2006, 2007; Konrad *et al.* 2008; Chapter 9), although "hydroecological associations remain poorly quantified" and studies on the topic few (Monk *et al*. 2006, p. 595). Surprisingly seldom have studies of low flows paid sufficient attention to characteristics of the natural flow regime or how they have been altered with flow reduction, when inferring or quantifying invertebrate response (Poff and Ward 1989; Tharme and King 1998; Extence *et al*. 1999; Lake 2000; Boulton 2003; Monk *et al*. 2007; Konrad *et al*. 2008). Moreover, relationships among multiple flow indices and measures of invertebrate response have infrequently been examined in relation to such disturbance. While promising initiatives continue to advance, most of the effort still remains directed at identifying individual high or low flow events, whether natural or artificial, that might constitute predictable or recognisable levels of physical disturbance to benthic invertebrates (Section 7.1).

Studies have addressed general measures of flow regime character and variability, such as the annual coefficient of variation (CV) and median discharge (Q_{50}), as well as high flows (e.g. annual maximum discharge (Q_{max}), flood frequency) and low flows (e.g. 95% exceedence flow, Q_{95}, and annual minimum flow, Q_{min}). With the limited evidence that annual average flows markedly affect aquatic ecosystems, the focus has increasingly turned to flow extremes (Bragg *et al.* 1999). In some instances, hydrological indices such as ambient discharge have been employed in conjunction with other environmental factors known to constrain community structure in the short-term (Boulton *et al.* 1992b). There has also been a resurgence in efforts to examine the ecohydrological significance of life history attributes in deriving relationships between flow variables, or measures of their alteration with disturbance, and invertebrate response (Lytle and Poff 2004; Poff *et al*. 2010; Chapter 9). In addition, attempts are ongoing to characterize ecologically meaningful flows more from a functional or process-related, rather than strictly structural, perspective (Choy 1998; Death *et al*. 2009). Whichever routes are pursued, the use of both conceptual flow-ecology models, to portray interrelationships between flow components and biotic responses, and statistical correlations between flow conditions and various species or ecosystem variables, has been advocated to enhance understanding (Petts 1996; Growns and Marsh 2000; Richter *et al.* 2006).

Exploring invertebrate response to short-term flow disturbance history

Characterization of invertebrate response to natural or artificial low flows in terms of the immediate dimensions of the disturbance has typically blended fairly short-term hydrological measures of the event (e.g. instantaneous discharge, Q_{inst}, or average daily discharge) with the abiotic effects generated. Conventionally, the latter have been described in terms of changes to physical habitat using hydraulic and/or habitat patch metrics, and in certain instances also water quality. With equally varying degrees of success, response to a disturbance event has been expressed simply using single flow indices that represent immediate or longer-period reach flow characteristics.

For instance, during a natural six-week summer period that encompassed the second-lowest discharge on record, the explanatory power of discharge and related abiotic factors in terms of run invertebrate response was higher in the nutrient-enriched Waipara River than the less altered Okuku River, N.Z., with nine versus only three community and taxon abundance metrics out of 14 correlated with the number of days at low flow, respectively (Suren *et al*. 2003). Invertebrate compositional changes with low flows were clearly in response to changes in physical habitat, with hydraulic radius an important predictor in both rivers, followed by wetted perimeter and velocity. While water quality was not incorporated, it was felt that certain assemblage change, in the Waipara R. especially, might have been indirectly in response to increased thermal stress. Relationships between family densities and a low flow index rating each site's tendency to be devoid of standing water in summer, as well as hydraulic and chemical variables, were established for invertebrate communities of multiple sites on naturally intermittent streams of the Guadiana River, Portugal (Pires *et al*. 2000). Tendency to dry, stream width, temperature and EC most influenced family abundances across the three streams, which displayed a wide range of variation in annual discharge. From among abiotic variables describing site general characteristics, discharge, hydraulics and alkalinity, many differences in invertebrate response among the biophysically similar Wissey, Rhee and Pang rivers, and between sites on each river experiencing natural or abnormally low flows (due to groundwater abstraction), could be related to taxon hydraulic preferences (Bickerton *et al.* 1993). Profiles of species hydraulic habitat preferences, constructed from a database of 21 U.K. rivers (Petts and Armitage 1991, cited in Bickerton *et al.* 1993), were used as a guide to potential flow indicator taxa and low flow responses. A group of families, including the Hydropsychidae, appeared in reduced numbers in the more severely low-flow affected Pang River than in the upper Wissey or Rhee. Riffle communities and certain taxa from above and below major abstraction points on four N.Z. streams were separated in ordination space along an axis that correlated negatively with discharge and 0.6V, and positively with EC and, to a lesser extent, periphyton biomass (Dewson *et al*. 2003).

The degree of influence of daily discharge as an individual index on the responses of benthic invertebrates, whether in terms of individual family densities or broader measures of assemblage composition, to different forms of low-flow disturbance appears limited and variable, based on the few instances in which this has been quantified (e.g. Gustard 1979; Dacova *et al*. 1992; Dudgeon 1992b; Armitage and Petts 1992; Armitage and Pardo 1995; Wood *et al.* 2000; Caruso 2002; Dewson *et al*. 2003, 2007a, b; Section 8.8.3). For instance,

a generally weak relationship between sampling-date daily discharge as a proportion of mean annual seven-day low flow (MALF) and a macroinvertebrate community index (MCI) was apparent for four rivers, among 12 N.Z. sites subjected to naturally extreme dry-season low flows with a one-year drought (Caruso 2002). Only insignificant moderate MCI decreases occurred with discharge reduction below MALF, as a result of small changes in species composition, reaching 10-15% below normal values in the subregion subjected to lowest discharges. Caruso (2002) speculated that the factors responsible for the decline in biotic scores were likely linked to flow-related modification of physical habitat and its hydraulic characteristics, supporting a need to incorporate abiotic measures reflecting more immediate site state.

Characterizing ecologically relevant flows using invertebrate relationships with long-term flow disturbance

Investigations of invertebrate response in relation to longer-term aspects of flow disturbance history have centered on relationships between invertebrate assemblages and flow statistics that typically span daily and monthly to annual/inter-annual timeframes, for individual rivers or multiple rivers of different regime types (Townsend *et al*. 1987, 1997a; Biggs *et al.* 1990; Jowett and Duncan 1990; Armitage and Petts 1992; Bickerton 1995; Castella *et al*. 1995; Feminella 1996; Englund and Malmqvist 1996; Clausen and Biggs 1997, 2000; Extence *et al*. 1999; Wood *et al*. 2000; Whittington 2000; Ruse and Davison 2000; Growns and Growns 2001; Riseng *et al.* 2004; Monk *et al*. 2006, 2007; Konrad *et al*. 2008). Hydrological measures have been largely derived from time series of natural average daily discharges, with the potential of records of altered discharges largely unexplored (but see Poff *et al.* 2010). While the flow statistics employed have varied tremendously across studies without much standardisation (see also Section 4.1.2), the basic approach appears fairly consistent. Abiotic factors other than flow are less commonly incorporated, presumably because such disturbance descriptors are seldom at a matching temporal scale. Although ecohydrologists continue to venture more deeply into this area, explicit connection of water quality or geomorphic time series with invertebrate response remains scarce. Even in environmental flow science, where habitat series are generated for invertebrates under scenarios of changing flow patterns (Waddle 1998a), physical habitat has tended to be described according to immediate hydraulic state rather than historical trends.

In a seminal approach to identify the most ecologically relevant of 34 different hydrological indices for characterizing flow regimes for benthic invertebrates (and periphyton), the degree of variance in invertebrate communities that could be explained by flow regime was ascertained for 83 N.Z. river sites (Clausen and Biggs 1997). Most indices reflected overall flow variability and general flow pattern, or focused on flood disturbance. Only Q_{90} and the Mean Annual Minimum (MAM), both standardised by Q_{50} for comparison across hydrological regimes, directly reflected low-flow disturbance. Of the biological metrics examined, benthic density most often strongly correlated with the typically annual-scale flow indices while species richness, followed by Shannon diversity, showed weaker relationships. Indices reflecting average flows and some measure of flow variability or predictability were clearly linked to most biotic indices. In a similar approach for 83 English and Welsh rivers, first grouped in terms of expected flow response on the basis of

similarities in regime type, relationships were modelled between macroinvertebrate community metrics at family level and 201 monthly and annual flow regime descriptors identified from various ecohydrological studies (Monk *et al*. 2006). Preceding 12 months of daily discharges were paired with low-flow season Biological Monitoring Working Party (BMWP) scores and Average Score Per Taxon (ASPT) values (both more typically water quality indicators - Armitage and Petts 1992; Wright *et al.* 1996), as well as Lotic-invertebrate Index for Flow Evaluation (LIFE) scores reflecting locally developed taxon tolerances for mean velocity ranges as a measure of biotic response to flow over time (Extence *et al*. 1999). Numerous significant correlations were evident among the suite of flow variables and LIFE and ASPT metrics reflecting an 11 year period, as well as where the data were stratified by hydrograph magnitude, shape or composite class, allowing up to 76% of overall ecological variance to be explained (Monk *et al*. 2006). The BMWP scores were weakly correlated with flow indices and hence discarded. An equally diverse suite of streamflow characteristics and regional regime types were examined across numerous western U.S. stream sites, to identify which flow indices acted most as limiting factors on predominantly dry-season riffle assemblages (Konrad *et al*. 2008). Thirteen of an original 50 flow indices reflecting aspects of high, low, and central-tendency flows showed strong relationships with 14 invertebrate metrics, exerting positive or negative upper or lower limits on assemblage composition, based on quantile regression. These biologically influential hydrologic metrics spanned daily to inter-annual scales, with each invertebrate index showing a distinct response to at least one of them. For invertebrates from multiple sites on a single river, the N.Z. Taieri R., in contrast, there were no significant relationships between the flow indices discharge CV, discharge variance and flood frequency, and taxon richness (Townsend *et al*. 1997a). For species traits known to link with flow disturbance (derived from Townsend *et al*. 1997b) however, high adult mobility (resilience trait) showed significant but weak relationships with discharge variance and CV, and streamlined-flattened larval morphology (resistance trait) showed a similar relationship with discharge CV.

In one of few studies focused on natural long-term flow disturbance gradients that incorporated additional abiotic factors, variation in the structure of riffle assemblages was related to a gradient of flow permanence from fully perennial to intermittent, across six neighbouring tributaries of the Upper Coosa River, U.S.A. (Feminella 1996); a composite index of rainfall plus direct observations was used to derive flow indices, due to the absence of streamflow records. Streams were ranked in terms of their flow disturbance history based on a combination of Q_{50}, and minimum discharge and mean wetted riffle area at summer baseflow. Despite a wide range in flow permanence, differences in assemblage composition were slight across streams with 75% of species, including the majority of rheophiles, present in all streams or without an obvious distribution pattern with respect to flow characteristics. Some predictable, albeit subtle relationships with stream permanence were evident, however, with several species exhibiting density trends obviously associated with historical low-flow disturbance. In another study addressing natural disturbance gradients using flow and other abiotic indices, the effects on invertebrate community structure of high and low flows, coupled with nutrient effects, were modelled across 133 riffles in 97 midwestern U.S. streams of differing hydrological regimes (Riseng *et al.* 2004). Differences in interregional hydrologic disturbance regime lead to distinct

structural differences in benthic communities. Low-flow disturbance alone, quantified using standardised Q_{90} and summer water temperature, was found to have only a small insignificant effect on grazers, yet more than four-fold stronger negative effects on filter-feeders. Several marked effects on invertebrate functional feeding groups were attributable to high flows (using flood-based indices of substratum movement) or a combination of high and low flow characteristics.

Flow variability expressed as CV, median discharge, specific yield and catchment area, as well as water chemistry, were secondarily important to other catchment-based parameters in differentiating among five ecoregional river groups, in a study to derive models for predicting effects of altered flow regimes on aquatic invertebrates across 144 New Zealand river sites (Biggs *et al.* 1990). Links between flow variability and hydraulic habitat, water quality, and the distribution and abundance of benthic invertebrates were examined by Jowett and Duncan (1990), for New Zealand rivers classified on the basis of their hydrological regime characteristics (Chapter 4). Significant correlations with the coefficient of flow variability (CVFLOW), as well as differences among river groups categorised as of low, medium or high variability, were found for 22 environmental variables. Distinct associations existed between two major invertebrate groupings and flow variability, with communities characterised by molluscs, chironomids or Oligochaeta more common in rivers with more variable flow regimes, while fauna dominated by trichopterans and mayflies predominated in less flow-variable rivers of high water quality. Of 20 environmental parameters, a stability index of physical disturbance that incorporated a range of hydrological (indirect, high-flow focused geomorphic descriptors), hydraulic, and thermal variables shown to affect invertebrate distribution and abundance, was the single best predictor of the number of riffle species in ten hydrologically different Waimakariri River tributaries and one lakeshore habitat in New Zealand (Death and Winterbourn 1994, 1995; Death 1996a). Over an extended 20-year period in the Thames River, England, mean annual discharge, followed by maximum total organic nitrogen, was the most important correlate of ten different flow, physical habitat and chemistry variables related to variations in chironomid taxon abundances (Ruse and Davison 2000).

Moving beyond ecohydrological characterization based principally on natural flow patterns, relationships between existing invertebrate community data and low-flow disturbance history were examined for 45 sites on the River Glen, a U.K. river increasingly impacted by anthropogenic flow reduction and drought-induced drying events (Bickerton 1995). Flow disturbance history was reflected by the summer seven-day average discharge (or Dry Weather Flow, DWF) of the year of sampling and the previous year, the additional low flow index, April mean daily flow, and the wet-winter 7-d high flow. Low flow indices were the best predictors, with strong to moderate correlations with community structure and taxon presence/absence. Interannual flow variability was also an important factor in the differentiation of river sites and the composition of their invertebrate communities. The relative influence of 48 different flow indices in explaining variation in invertebrate communities with low-flow disturbance, due to multiple periods of severely reduced flows with drought, was examined in the perennial U.K. chalk river, the Little Stour (Wood and Petts 1994, 1999; Wood *et al.* 2000). The indices reflecting flow disturbance history, most at monthly

scale, were: monthly mean, minimum and maximum discharges for a year preceding invertebrate collection; mean daily discharge at time of sampling, and for seven days prior; and maximum monthly discharges, for 12-, 6- and 3-months pre-sampling, and the DWF, to represent high and low flow extremes, respectively. Of all flow indices, 18 showed pronounced correlations with some measure of assemblage composition. Persistence of benthic invertebrate communities, based on correlations between taxon abundances and physical and chemical variables for two surveys eight years apart, was significantly negatively associated with range in discharge magnitude for Plecoptera and with minimum discharge for non-insect taxa, for 27 riffle sites in the Medway and Sussex Ouse headwaters, England (Townsend *et al*. 1987). As both surveys were conducted in very dry years where low flows affected the biota of other British rivers, it was postulated that the observed marked variation in persistence might relate in some part to differences in drought responses among sites.

For multiple sites on 22 British rivers spanning a range of natural river types and different abstraction effects, discharge, baseflow and substratum composition dominated in explaining variation in invertebrate family-level abundance, richness and other biotic measures (Armitage and Petts 1992). In another study of 22 U.K. rivers also subjected to varying kinds and degrees of water abstraction, regional factors (especially the upland-lowland distinction) were considerably more influential than any localised flow reduction effects with water abstraction over two summer periods, based on relationships among 89 invertebrate taxa and 16 environmental variables encompassing flow indices, habitat hydraulics, chemistry and catchment characteristics (Castella *et al*. 1995). No distinct patterns of taxon response to discharge reduction could be elucidated for a baseflow index (mean discharge/Q_{95}) or instantaneous abstraction index. Refined analysis for rivers of the same basic biophysical type using environmental variables found to be most closely linked to flow reduction effects, including discharge, depth and velocity, was somewhat more effective in characterizing invertebrate response. For four groundwater-dominated lowland rivers, distinct invertebrate responses were principally attributed to hydraulic-thresholds, namely a wholescale decline in velocity below 0.05 m s^{-1} and in depth below 0.10 m, as well as reduction in macrophyte cover and increased fines, in the flow-impacted reaches. The more regular flow regimes of such rivers may have rendered their invertebrate assemblages more susceptible to extreme summer low flows than the biota of other rivers examined. Flow regimes for sites with unaltered flow regimes and sites subjected to two types of flow regulation within the Hawkesbury-Nepean River System, Australia, could be differentiated using seven of nine hydrological indices calculated from preceding six-month discharge records (Growns and Growns 2001). In addition to CV, the low flow indices baseflow index, median daily discharge difference, minimum daily discharge and number of zero-flow days were most influential; maximum daily discharge and flood frequency showed little effect. The indices of baseflow and daily rate of change in discharge correlated most strongly with invertebrate response. The gradient of flow regime alteration exerted more effects on invertebrate communities than did water quality, with 24 of a total of 297 taxa indicative of natural flow regimes and adversely affected by flow regime change, while nine benefited from unnatural flow disturbances. Of 11 flow variables that best differentiated ‘unregulated’, ‘regulated flow pattern’, and ‘reduced flow’ regime

types of Swedish rivers, maximum flow increase (%) was most influential in reflecting flow reduction impacts on the richness and abundance of invertebrate functional feeding groups, with clear responses by the benthos only evident outside the index's natural range (Englund and Malmqvist 1996). Although model outcomes suggested that single extreme events might be critical, all variables describing flow variability were intercorrelated and negatively correlated with invertebrate response, such that it was not possible to definitively ascribe the disturbance effects to any single flow effect.

Setting ecohydrological objectives for river management

A number of other ecohydrological approaches based on invertebrate response to low-flow disturbance, in addition to those described above and ecohydraulics-based efforts (Section 8.1.2), have been adapted or specifically developed to identify ecological flow objectives for river management (Tharme 1996; 2003; Arthington 1998a; Dunbar *et al*. 1998; Extence *et al*. 1999). Some illustrative examples are provided here, with a full treatment of the topic beyond the scope of this chapter (see also Section 1.5, for an introduction). Holistic environmental flow methods, where arguably the greatest advances have been made in explicitly linking hydrology and invertebrate ecology to date, are detailed in Arthington (1998a), King *et al*. (2000) and Tharme (2003).

Multivariate statistical approaches using invertebrate scores for rapid bioassessment of river impairment, derived from comparisons of unregulated and variously regulated sites, while not originally designed for assessing the impacts of different flow regimes have been adapted for this purpose (Bullock *et al.* 1991; Tharme 1996; Dunbar *et al*. 1998; Arthington 1998a; Choy 1998; Extence *et al*. 1999). Jones and Peters (1977, cited in Dunbar *et al*. 1998; Extence *et al*. 1999), for example, undertook a desktop regional statistical analysis where flow regimes of 43 rivers, from which invertebrate data were routinely collected, were characterized on the basis of average seasonal flow pattern, ratio of maximum to minimum flows for different seasons, time and quantity by which average daily flow was exceeded, rate of change of flow, and average velocity (0.6V) at mean daily flow. Distinct relationships were generated between the various flow variables and particular invertebrate communities. Within England's Surface Water Abstraction Licensing Procedure for setting environmental flows, Kirmond and Baker (1997, cited in Bragg *et al*. 2005) produced an environmental weighting system based on scoring for river type and ecological sensitivity to low flow conditions, with a scoring system for 48 invertebrate taxa that ranked them in terms of their tolerance to flow reduction. The Scott Wilson Kirkpatrick scoring method, developed specifically for addressing flow needs of British rivers during summer low flow periods, integrates two composite ecohydrological indices (Dunbar *et al*. 1998; Extence *et al*. 1999). The ecological index considers an invertebrate assemblage score (ASPT) and expert assessment, while the hydrological index relates groundwater abstraction/recharge, surface water abstraction/Q_{95} and 'residual seasonal flow' to a minimum ecologically acceptable flow which may be seasonal. Choy *et al.* (2000) developed a 'community composition approach' to determine environmental flows for benthic invertebrates within a Flow Restoration Methodology (FLOWRESM; Section 1.5) application for the Brisbane River, Australia. The functional composition and diversity of invertebrate

assemblages of different habitat types of downstream regulated and upstream unregulated sites were compared, and observed biotic changes related to differences in hydrological, hydraulic habitat and other biophysical descriptors.

Various ecohydrological methods were applied to assess the impacts of abnormally low flows and finally, drying, on the middle reaches of the River Glen, eastern England, and to identify environmental flows to restore river condition (Petts *et al.* 1995). Hydrological approaches relied on the low flow index Q_{95} (for an average rainfall year), 10% to 30% of average daily flow to maintain habitat conditions (as per Orth and Leonard 1990), and a flow recession approach that yielded a Q_{93} estimate for an expected extreme-flow year. A breakpoint in the discharge-wetted bed area relationship for a representative reach was used to recommend a minimum flow for maintaining optimum physical habitat. Additionally, an empirical model based on relationships between invertebrate Biological Monitoring Working Party (BMWP) scores for multiple river sites and a series of best-fit abiotic attributes describing habitat hydraulic quality and quantity under low flows, and water quality variables, was used to recommended a minimum flow to maintain the invertebrate community. The Basque method was used to develop environmental flows to maintain invertebrate (and fish) species diversity in the summer-autumn period in Spanish rivers, using one of two relations (Docampo and De Bikuña 1993). For upper, unpolluted stream reaches, a biotic equation was adopted, derived from a diversity spectrum which relates the number of invertebrate species to natural geometric mean discharge, calculated incrementally along the river (Dunbar *et al*. 1998; Bragg *et al*. 2005). The optimum instream flow was determined as the natural flow which resulted in a reduction in species diversity of one unit, and the absolute minimum flow was calculated similarly, considering only the lowest flow period. In modified lower reaches, a discharge-wetted perimeter (WP) model calibrated at low flows was used to determine a minimum acceptable discharge based on protection of 60% WP (Dunbar *et al*. 1998) or the WP required to maintain 15 or more taxa (Bragg *et al*. 2005). Links among discharge, functional habitat availability and invertebrate production were used to develop optimum and minimum environmental flows for the North Italian Pioverna River, in the Benthic Habitat for Optimum Flow Reckoning approach (BENHFOR; Buffagni 2001). Invertebrate production values were determined for four functional habitats identified on the basis of assemblage composition. Field mapped changes in habitat type occurrence were quantified for multiple discharges and used to derive habitat area-discharge relationships. Expected secondary production for the entire assemblage, single taxa, or guilds, was predicted by combining the production estimates for different functional habitats with the discharge-related relative occurrence of each habitat. On the resultant production-discharge curves, such as were constructed for the mayfly, *Ecdyonurus helveticus,* breakpoints could then be used to identify optimum and minimum acceptable flows for invertebrates.

In the Dundee Hydrological Regime Assessment Method (DHRAM; Section 1.5.3), the risk of impacts on riverine biota from hydrological regime alteration of 11 Scottish rivers was assessed using hydrological change thresholds calculated for ten flow indices derived from the means and CVs for the five main Indicators of Hydrologic Alteration groups (Black *et al.* 2002). The results were used to assign rivers to one

of five classes of severity of impact compatible with the Ecological Status Classification of the E.U. Water Framework Directive. Development of a calibration system was proposed to enable a site to be compared with other biophysically similar systems with differing degrees of hydrological disturbance, for cases of limited biological data for DHRAM validation. Within the U.K. Catchment Abstraction Management Strategies (CAMS) process, environmental flow estimates for water permitting have depended upon explicit connection of a standard low flow index, Q_{95}, with diverse measures of biophysical condition (Dunbar *et al*. 2004; Section 1.5). A novel approach, the Flow Stressor-Response (FSR) method, relies on relationships between invertebrates known to be sensitive to flow-related hydraulics (Section 8.1.2) and changes in key hydraulic factors (and potentially also biotope metrics) under various flow regimes, rather than solely on direct links between taxa and flow indices, to characterize biotic response to flow alteration (O'Keeffe *et al*. 2002). In an application of the FSR method for the South African Crocodile River, as part of a holistic environmental flow determination (Section 1.5), a generic index of low flow-related stress based on relative changes in hydraulic habitat (WP, 0.6V, etc.) was adopted (O'Keeffe *et al*. 2002, p. 86, Table 1). Six Trichoptera and Ephemeroptera sensitive to extreme low flows in another part of the Incomati System were used as the flow-dependent indicator taxa (for which changes in abundances, life stage viability and local persistence with flow were evaluated), along with reach discharge reduction-hydraulics relationships, to develop the natural (reference) and extreme low-flow stress curves. The curves were used to translate flow regimes into stress (disturbance) profiles (magnitude, frequency, duration) reflecting short-term habitat alteration, that allowed various flow scenarios to be contrasted in terms of degrees of departure from natural low flows and hence, potential risk of change in invertebrate composition. In the renowned Lotic-invertebrate Index for Flow Evaluation method, explicit relationships were developed between streamflow regime and benthic composition (using routine invertebrate monitoring data) and then used to characterize ecologically meaningful flows for invertebrates and set hydroecological objectives for U.K. rivers (Extence *et al*. 1999; Section 1.5). Most benthic macroinvertebrate species and families from riffle sites across the U.K. were assigned to one of six flow groups based on their recognised primary associations (reflecting known mean-velocity tolerance ranges, where appropriate) with drying/drought-impacted sites or those with rapid flows, as well as scored based on their relative abundances. LIFE scores were then calculated for sites, such that higher flows should result in higher scores for assemblages. Influential flow regime features for invertebrate communities could then be identified using the most significant correlations between several hundred different flow indices, calculated from streamflow records reflecting flow history, and LIFE scores, for a wide range of regional river types. Interestingly, different flow indices were found to be most influential in characterizing invertebrate communities at species and family taxonomic levels, both within and across a range of flow regime types. While LIFE scores were useful for characterizing flows for invertebrates in England and Wales (Monk *et al*. 2006, 2007; see above), early results were inconclusive in linking hydrological impact classes with biological data for Scottish rivers (Black *et al.* 2002). Extence *et al*. (1999) felt that further development of the LIFE approach might enable the definition of generalised invertebrate-flow responses for specific river types, as well as thresholds to conserve invertebrate diversity in

individual rivers, underscoring a potential link between this approach and those of Konrad *et al.* (2008) and Poff *et al.* (2010), for instance, aimed at extracting generic flow-ecology relationships (Chapter 9).

8.2 APPROACH AND OBJECTIVES

The extent to which the kinds of invertebrate responses identified in Chapter 7 were a function of indirect, flow-mediated changes in biotope-specific hydraulic habitat, water chemistry, individual flow measures and longer-term hydrological history, is the main subject of Chapter 8. Previous chapter results were drawn upon to integrate low-flow disturbance effects and biophysical responses, to fulfil primary thesis objectives 5-7 (Section 1.2). The focus was on the following objectives, to:

1. Determine the degree of biotope specificity of invertebrate taxa at low flows.
2. Identify the physical habitat variables that are most important in determining the distributions and abundances of invertebrate taxa, and hence assemblage composition at low flows.
3. Determine the tolerance ranges of invertebrate taxa for hydraulic habitat variables and their changes under low flow conditions.
4. Identify invertebrate taxa and measures of assemblage composition that are most responsive to discharge reduction, and might therefore represent useful indicators of low-flow disturbance.
5. Characterize ecologically relevant low flows for invertebrates, by linking key flow indices with invertebrate responses to, and physical changes in, habitat conditions at low flows.

The analytical methods employed are documented in Section 3.5.2. Biotope specificity analyses (Section 8.3) and assessments of the relative tolerance of invertebrates for habitat hydraulics (Section 8.4), including through the use of HSI curves, were used to identify invertebrates that showed preferences for particular biotopes and hydraulic factors, under natural and extreme low flows. In Section 8.5, direct relationships between individual taxa and measures of diversity, and discharge magnitude, were explored. These first results (Sections 8.3-8.5) aimed at confirming (building on preliminary findings in Chapter 7) those taxa particularly sensitive to low flow conditions, and the possible mechanisms underlying responses. Subsequently, interrelationships between a suite of abiotic variables and responses by assemblages and potential flow-indicator taxa were sought in relation to low-flow disturbance at ecologically meaningful scales (Section 8.6). Variables used were representative of: (i) reach-scale physical habitat (identified in Chapter 6); (ii) water chemistry (identified in Chapter 5); and (iii) select indices of low flow and hydrological variability at three different temporal scales (identified in Chapter 4). The chapter concludes with a discussion on some of the central outcomes of these efforts to characterize ecologically relevant low flows for invertebrates (Section 8.7).

8.3 LOW-FLOW DISTURBANCE AND INVERTEBRATE BIOTOPE SPECIFICITY

8.3.1 Biotope specificity of invertebrate families

Biotope specificity under natural low flow conditions

The results of Kruskal-Wallis ANOVAs of the extent of biotope specificity of individual families and higher taxa at natural low flows showed strong support for assemblage-based patterns (Section 7.4), with 20 families exhibiting highly significant biotope preferences (actual utilisation; Section 3.5.2) on the basis of relative abundances, and a further ten showing significant associations with individual biotopes (Table 8.1). Thus, 58% of all families exhibited distinct biotope type preferences at natural dry-season flows (see also Section 8.4). All families found to be useful discriminant taxa for different biotope assemblages at low flows (see Section 7.4) showed highly significant degrees of association with one or more biotopes (Table 8.1). There were few cases, however, where invertebrates were exclusive to a single biotope type, and then only for pools. Results were based on combined data from all sites, supporting the earlier conclusion that the biotope is a generic, ecologically meaningful unit at low flows (Section 7.8.2).

Highly significant preferences among all major biotopes were only encountered for the Simuliidae ($H = 127.342$, $P = 0.000$; see also HSI curves below) and Hydropsychidae ($H = 88.376$, $P = 0.000$), both of which showed a marked preference for riffles, significantly reduced preferences for runs, and low tolerances for pool environments (Table 8.1). A further six taxa differentiated strongly between riffles, and runs and pools, showing significantly higher natural densities in riffles. Most notable were the Elmidae, as well as acarinids, Chironomidae, Baetidae, Philopotamidae and Oligochaeta. Three other taxa, namely Aeschnidae, cnidarians (*Hydra* spp.), and Glossosomatidae (*Agapetus* spp.) were at significantly elevated densities in faster-flowing biotopes, while altogether absent from pools. Significantly lower numbers of leptocerids (supported by HSI curves below) and Teloganodidae occurred in riffles than in either runs or, particularly pools. In addition, corixids, caenids and notonectids showed highly significant preferences for pools (Table 8.1). Of these families, only the Notonectidae, well recognised as pool dwellers (Scholtz and Holm 1985; De Moor *et al.* 2003b; Picker *et al.* 2004), were entirely absent from riffles. Coenagrionids, dytiscids and naucorids were entirely absent from both riffles and runs, also representing specialist slow-flowing or standing-water families (Table 8.1). Runs tended to represent patches of intermediate to marginal suitability for the majority of invertebrate families, for those that preferred riffles or pools. The Heptageniidae was the sole family that appeared to prefer runs (Table 8.1), though with no significant difference detected between densities in pools or riffles (multiple comparison tests). Twenty-two generalists showed no significant preference for a particular biotope(s), including several coleopteran, dipteran and trichopteran families (Table 8.1 footnote). In some cases, small numbers of occurrences possibly limited the extent to which biotope preferences were evident.

Table 8.1 Biotope specificity of invertebrate families at natural low flows, based on significant Kruskal-Wallis ANOVA results ($P \leq 0.05$). N = 324 (108 samples per biotope, pooled for all sites and months). *** = highly significant ($P \leq 0.001$). *Post hoc* comparisons were used to identify which biotopes were significantly different, as delimited by shading. Diagonal hatching indicates non-significant results for adjacent biotopes, but significant differences between riffles and pools. ^{NSP} and ^{NSR} indicate non-significant differences between riffles and pools. Absence of shading denotes cases where results were non-significant across all biotope pairs. Biotopes with the highest (+), lowest (-) or zero (0) mean abundances 0.1 m^{-2} are indicated.

FAMILY	H	*P*	RIFFLE	RUN	POOL
Simuliidae***	127.342	0.000	+		−
Hydropsychidae***	88.376	0.000	+		−
Elmidae***	81.141	0.000	+		−
Acarina***	75.949	0.000	+		−
Chironomidae***	69.112	0.000	+		−
Baetidae***	61.071	0.000	+		−
Hydroptilidae***	31.883	0.000	+		−
Athericidae***	31.779	0.000	+		−
Philopotamidae***	31.626	0.000	+		−
Leptoceridae***	28.702	0.000	−		+
Oligochaeta***	27.711	0.000	+		−
Hydraenidae***	23.182	0.000	+		−
Corixidae***	22.902	0.000	−		+
Heptageniidae***	20.889	0.000	NSP	+	− NSR
Empididae***	18.819	< 0.001	+		−
Caenidae***	18.048	< 0.001	−		+
Notonectidae***	17.130	< 0.001	0		+
Pyraustidae***	16.475	< 0.001	+	−	
Teloganodidae***	16.124	< 0.001	−		+
Aeschnidae	10.704	0.005	+		0
Collembola	7.427	0.024		+	−
Corydalidae	7.253	0.027	+		−
Cnidaria	7.147	0.028	+		0
Nematoda	6.737	0.034	+		−

Table 8.1 Continued.

FAMILY	H	*P*	RIFFLE	RUN	POOL
Notonemouridae	6.225	0.044	+	−	
Glossosomatidae	6.163	0.046	+		0
Coenagrionidae	6.037	0.049	0	0	+
Dytiscidae	6.037	0.049	0	0	+
Naucoridae	6.037	0.049	0	0	+
Helodidae	5.982	0.050	+		−

Taxa for which no significant inter-biotope differences in abundance were found: Barbarochthonidae; Blepharoceridae; Ceratopogonidae; Culicidae; Dixidae; Dryopidae; Ecnomidae; Ephemeropteran juveniles; Gomphidae; Gyrinidae; Hebridae; Hydrophilidae; Leptophlebiidae; Libellulidae; Limnichidae; Mesoveliidae; Petrothrincidae; Playthelminthes; Polycentropodidae; Sericostomatidae; Tipulidae; Veliidae.

Biotope specificity at extreme low flows

Under conditions of manipulated extreme low flows, there was a dramatic decrease in the number of families with detectable among-biotope preferences, by 20 families (Table 8.2). Furthermore, of the ten families still exhibiting some specificity, typically there was a loss in their degree of association with biotopes of different types. Simuliids still showed the greatest biotope-association of all families, but the distinction observed at natural flows between numbers in runs and pools was lost. Chironomidae showed a shift from preferred riffle patches, to slower-flowing but more abundant runs (Chapter 6). Similar trends were apparent for baetids, acarinids and elmids. Though still most abundant in riffles, hydropsyschids exhibited a pronounced decrease in association with particular biotopes from that observed under natural summer discharges (Table 8.2). The biotope associations of Leptoceridae (see also HSI curves below) and Athericidae also decreased at extreme low flows, in the latter family with a shift in abundances from riffles into runs. Empididae declined to zero in both pools and runs, but also occurred in low densities in both biotopes under natural flows. Riffles still appeared marginally suitable for Teloganodidae at abnormal discharges, but there was a shift from pools into runs.

8.3.1 Biotope specificity of Chironomidae species

Biotope specificity at natural low flows

Twelve and five chironomid species (i.e. 38% of the approx. 45 species in total from all sites; Appendix 7.8) exhibited highly significant and significant associations, respectively, with specific biotopes (Table 8.3). Four of these chironomid species or species groups showed highly significant biotope affinities (i.e. for within-biotope microhabitats), on the basis of abundances, across all of the biotopes under natural low flows (Table 8.3). Of this sub-group, *Notocladius capicola* showed the greatest biotope specialisation, with a strong preference for riffles and very limited use of pool environments (H = 104.392, *P* = 0.000; also

supported by HSI analysis below). *Rheotanytarsus fuscus* (H = 51.349, *P* = 0.000) and *Cricotopus* spp. (H = 43.692, *P* = 0.000) also showed more intensive use of riffle patches, than runs or, in particular, pools. *Tvetenia calvescens* and *Rheocricotopus capensis* showed similar patterns. *Thienemanniella lineola* (H = 43.952, *P* = 0.000), while also showing limited preference for pools, was on average most abundant in runs.

Table 8.2 Biotope specificity of invertebrate families midsummer with extreme flow reduction, based on significant Kruskal-Wallis ANOVA results (*P* ≤ 0.05). Samples subjected to experimental flow reduction during the impact phase were pooled across months and sites. *N* = 54 (18 samples per biotope). *** = highly significant (*P* ≤ 0.001). *Post hoc* comparisons were used to identify which biotopes were significantly different, as delimited by shading. Diagonal hatching indicates non-significant results for adjacent biotopes, but significant differences between pools and riffles. Absence of shading denotes cases where results were non-significant across all biotope pairs. Biotopes with the highest (+), lowest (-) or zero (0) mean abundances 0.1 m^{-2} are indicated.

FAMILY	H	*P*	RIFFLE	RUN	POOL
Simuliidae***	28.720	0.000	+		−
Chironomidae***	21.314	0.000	+		−
Baetidae	12.426	0.002	+		−
Acarina	11.641	0.003	+		−
Hydropsychidae	11.404	0.003	+		−
Elmidae	8.895	0.012	+		−
Teloganodidae	8.558	0.014	−	+	
Leptoceridae	6.904	0.032	−		+
Athericidae	6.393	0.041		+	−
Empididae	6.229	0.044	+	0	0

Significantly higher abundances in pools, than in the other biotopes, were apparent for the tanypods, *Ablabesmyia dusoleili* (as supported by HSI curves) and *Paramerina* spp., as well as for *Polypedilum* spp. to a lesser extent (Table 8.3). For *Polypedilum*, the bimodal distribution of individuals among biotopes suggested there might be sub-groups of species showing preferences for strong-flowing or slow- to non-flowing habitat patches. Tanypod juveniles and *Cryptochironomus* spp. were the sole taxa with a significant association with only pools. As at family-level, there were typically fewer species showing preferential utilisation of pools than riffles or runs. Lower species richness than that of other biotopes was typical of pools (Section 7.8), which supported the observation.

All chironomids tending to showing biotope-specific patterns of distribution under low flow regimes (Section 7.7.2), except *Thienemanniella trivittata*, exhibited highly significant biotope associations (Table 8.3), lending firm support to previous results. In some cases, biotope-species relationships were less clear

than those at family level, possibly at least in part due to a reduction in sample number (and hence, power of detection) in the former instance.

Table 8.3 **Biotope specificity of chironomid species at natural low flows, based on significant Kruskal-Wallis ANOVA results ($P \leq 0.05$).** N = 207 (69 samples per biotope, with data pooled for all sites and months). *** = highly significant ($P \leq 0.001$). *Post hoc* comparisons were used to identify which biotopes were significantly different, as delimited by shading. Diagonal hatching indicates non-significant results for adjacent biotopes, but significant differences between riffles and pools. ^{NSP} and ^{NSR} indicate non-significant differences between riffles and pools. Absence of shading denotes cases where results were non-significant across all biotope pairs. Biotopes with the highest (+), lowest (-) or zero (0) mean abundances 0.1 m^{-2} are indicated.

SPECIES	H	*P*	RIFFLE	RUN	POOL
*Notocladius capicola****	104.392	0.000	+		−
*Rheotanytarsus fuscus****	51.349	0.000	+		−
*Thienemanniella lineola****	43.952	0.000		+	−
Cricotopus spp.***	43.692	0.000	+		−
*Tvetenia calvescens****	42.749	0.000	+		−
*Ablabesmyia dusoleili****	37.170	0.000		−	+
*Rheocricotopus capensis****	34.328	0.000	+		−
Paramerina spp.***	26.101	0.000	−		+
Polypedilum spp.***	23.524	0.000		−	+
*Conchapelopia trifascia****	19.316	< 0.001	+		−
*Cricotopus kisantuensis****	17.623	< 0.001	+		0
Orthoclad sp. A***	15.976	< 0.001	+		−
Eukiefferiella clavigera	10.966	0.004	+	0	−
Thienemanniella trivittata	10.400	0.006	NSP	+	− NSR
Tanypod juveniles	10.196	0.006	0	0	+
Corynoneura spp.	9.658	0.008	−		+
Cryptochironomus spp.	8.117	0.017	0	0	+

Biotope specificity at extreme low flows

Under conditions of extremely reduced discharges (Table 8.4), five species no longer exhibited a significant association with one or more biotopes (of these, *Cryptochironomus* spp. and *Eukiefferiella clavigera* were absent from the sample subset). Of the 12 chironomids still showing specificity with flow perturbation, *Notocladius capicola* and *Cricotopus* spp. were the only species still exhibiting highly significant biotope preferences, for riffles (Table 8.4; see also HSI curves below). Generally, there was a marked breakdown in specificity below that found for natural low flow regimes (supporting Chapter 7 results), indicated by lower

significance values in all cases, a preponderance of non-conclusive *post hoc* tests for adjacent biotopes, and shifts in the biotope inhabited by fewest individuals for some species. Only two taxa emerged with enhanced biotope specificity at very low discharges (Table 8.4). *Nanocladius* showed a significant preference for pools at extreme low flows (naturally a characteristic pool species). *Cardiocladius hessei* showed an increase in biotope specificity with flow reduction, to a significant level, with greatest density in runs.

Table 8.4 Biotope specificity of chironomid species mid-summer with extreme flow reduction, based on significant Kruskal-Wallis ANOVA results ($P \leq 0.05$). Samples subjected to experimental flow reduction during the impact phase were pooled across months and sites. N = 54 (18 samples per biotope). *** = highly significant ($P \leq 0.001$). *Post hoc* comparisons were used to identify which biotopes were significantly different, as delimited by shading. Diagonal hatching indicates non-significant results for adjacent biotopes, but significant differences between riffles and pools. Absence of shading denotes cases where results were non-significant across all biotope pairs. Biotopes with the highest (+) and lowest (-) or zero (0) mean abundances 0.1 m^{-2} are indicated.

SPECIES	H	*P*	RIFFLE	RUN	POOL
*Notocladius capicola****	31.208	0.000	+		−
Cricotopus spp.***	16.486	< 0.001	+		−
Rheocricotopus capensis	11.562	0.003	+		0
Rheotanytarsus fuscus	11.523	0.003	+		−
Tvetenia calvescens	9.699	0.008	+		−
Conchapelopia trifascia	9.227	0.010	+		−
Ablabesmyia dusoleili	9.183	0.010	−		+
Thienemanniella trivittata	8.344	0.015		+	−
Cricotopus kisantuensis	8.111	0.017	+		0
Thienemanniella lineola	7.694	0.021	+		−
Nanocladius spp.	6.827	0.033		−	+
Cardiocladius hessei	6.229	0.044	0	+	0

8.4 INVERTEBRATE TOLERANCES FOR THE DYNAMICS OF HYDRAULIC HABITAT AT LOW FLOWS

8.4.1 Family hydraulic tolerances at low flows

General relationships at natural low flows

The results of Spearman rank order correlations indicated detectable, and in many instances highly significant, relationships between 38 of all invertebrate families assessed and one or more of the ten principal hydraulic factors used to characterize biotopes at low flows (Table 8.5). As anticipated, the majority of

hydraulic variables examined were highly significantly inter-correlated (r_s values, $P \leq 0.001$). Most especially, the complex variables Re and velocity to depth ratio (VD_{ratio}) were strongly associated with all other hydraulic habitat variables examined, on which they are based (Section 3.4.4). Additionally, Fr and turbulence index (TI) were correlated with all variables except depth and median substratum size, respectively. It was not surprising therefore, for instance, that a family showing a strong association with mean column velocity (0.6V) commonly showed similar relationships with NBV, or with derived variables such as Fr and VD_{ratio}, found useful for physically differentiating biotopes at very low flows (Section 6.4).

As families possessed different degrees of dependency on the array of variables that combined to reflect local hydraulic conditions at natural low flows (Section 8.5), it was possible to identify those families most directly responsive to local hydraulics and the variables with which relationships were strongest. As envisaged, highly significant and in many instances strong relationships with hydraulic factors were evident for all families that showed high biotope specificity, typically at R_s values above 0.40 (Table 8.5). The Hydropsychidae was the sole family significantly correlated with all hydraulic indices, except directly with depth. Densities of a further nine families or higher taxa were significantly positively correlated with seven out of the ten hydraulic variables examined under natural low flows: Acarina, Elmidae, Chironomidae, Empididae, Athericidae, Simuliidae, Baetidae, Oligochaeta, and Hydroptilidae.

Many families, including the above, showed strong positive relationships with the suite of velocity-related measures, from 0.6V to VD_{ratio}. Simuliids, not unexpectedly, demonstrated the strongest association with all velocity-based variables (r_s = 0.65 or 0.66, for pooled data). Strongly positively associations with complex hydraulic variables, such as TI, Re and Re_*, were shown by many families as well, principally the Simuliidae, Hydropsychidae, Chironomidae and Baetidae. Notable were the families exhibiting significant negative relationships with hydraulic variables, all of which showed a marked preference for pool and slow- to non-flowing environments (Table 8.1), namely Caenidae, Teloganodidae, Leptoceridae, Corixidae, Naucoridae and Notonectidae. Of these families, three (Corixidae, Notonectidae, Leptoceridae) were significantly correlated with a substantial seven hydraulic factors at naturally low flows.

By far the weakest associations between invertebrate families and habitat hydraulics at natural low flows were for water depth, relative roughness (and its inverse, relative exposure), and substratum size (already largely accounted for in faunal densities). Although depth, in particular, was one of the most influential variables in biotope characterization on physical grounds (Section 6.4), the benthos reacted to less direct, more complex representations of depth, though relatively weakly in many cases, through variables such as VD_{ratio}, TI, Re_* and Re.

Site-specific relationships of invertebrate families with different hydraulic factors

For individual sites, natural relationships between variations in family abundances and hydraulic variables showed the same general trends as obtained for all sites in combination, but were typically intensified (elevated r_s values, Table 8.5).

For the Elands River, fewer families showed highly significant correlations than when data from all sites were pooled. Some taxa, such as the Blepharoceridae, exhibited highly significant relationships with hydraulic conditions at a site, but not when data were combined (quite possibly an influence of taxon absence at some sites). In contrast, the Simuliidae and Baetidae showed weaker relationships with hydraulics than when sites were considered in combination. The Molenaars site showed stronger-fit relationships between especially the Chironomidae and Simuliidae, and hydraulic habitat, than at other sites. Higher r_s figures than for pooled data were recorded for the Baetidae, Pyraustidae, Chironomidae, Simuliidae and Philopotamidae for most key variables. Many more taxa showed highly significant correlations with hydraulics for the Du Toits than for the other reaches. Higher correlations than general were found for the Acarina, Elmidae, Collembola, Empididae, Athericidae, Leptoceridae, Caenidae and Nematoda. Similar or higher r_s values to those of the Du Toits were found at the Riviersonderend site, for Elmidae and Leptoceridae, and lower than at either the Molenaars or Du Toits, for the Simuliidae. At the Riviersonderend, significantly higher associations with several hydraulic variables than general were observed for notonemourid stoneflies, suggesting they might have potential as a flow-responsive indicator for this particular river. Higher correlation values than obtained at other sites were found for baetids, and values below those of other sites for the Hydropsychidae.

Shifts within family hydraulic tolerance ranges with extreme flow reduction

At extreme low flows, for all impacted sites combined, the majority of taxa no longer exhibited highly significant links to local patch hydraulic conditions (Table 8.5). Declines in the numbers of significant relationships with family densities were most severe for velocity to depth ration (VD_{ratio}, from 18 at natural dry-season flows to only four with abnormal flow reductions), Fr and Re_*, closely followed by all other variables with which invertebrates had been strongly associated at naturally low discharges.

Hydropsychidae showed a marked decrease in the number of significant positive hydraulic relationships with density from nine to five. Only two families out of the 13 with the most numbers of significant correlations at natural flows retained all their significantly positive density-hydraulics relationships, namely Simuliidae and Chironomidae. For the Elmidae, Chironomidae, Simuliidae and Baetidae, for those hydraulic factors with which there remained highly significant relationships with abundances at severely reduced discharges, there were consistent increases in correlation strength. In contrast, none of the originally significant, positive hydraulic relationships retained significance for Empididae, Athericidae, Hydroptilidae or Oligochaeta. Furthermore, none of the multiple significantly negative hydraulics-density relationships for the most

hydraulically influenced slow-water families, Leptoceridae, Corixidae and Notonectidae, remained so at experimentally reduced discharges.

Hydraulic tolerance ranges for indicator families

On the basis of the above relationships of different families with biotopes and microhabitat conditions, and considering the variables found to be most influential in the physical discrimination of biotopes at low flows, natural tolerance ranges were determined for select indicator families and hydraulic variables (see Appendix 8.1 for specific ranges). Mean tolerance values were found to be more informative than maxima and minima (also the case at species level - see below), for identifying general trends. Calculated ranges chiefly showed a separation based on depth, between families preferring very shallow waters (e.g. Hydropsychidae, Notonectidae) and those inhabiting slightly but significantly deeper habitats (e.g. Empididae, Teloganodidae). Similarly, pool taxa separated from those preferring riffles on the basis of average and near-bed velocities and, to a lesser extent, Froude numbers.

Habitat suitability index curves provided an alternative and more useful way of examining taxon hydraulic tolerange ranges and their dynamics with discharge. Suitability curves for habitat utilisation and preference were constructed and compared with habitat availability (pooled across sites and months; Section 3.5.2) for the Simuliidae and Leptoceridae, as two indicator taxa which usefully illustrated the extremes of flow response observed across the riffle-pool continuum. Curves were produced for two hydraulic variables for which particularly strong correlations with invertebrate densities were found (i.e. NBV, Fr), with responses to natural and extremely low flow conditions contrasted in each case.

Despite the preponderance of low to zero near-bottom velocities at natural low flows, Simuliidae more intensively utilised a range of higher velocities to well above 0.60 m s^{-1} (Figure 8.1a). The corresponding preference curve, factoring hydraulic habitat availability into account, indicated a narrow range of optimum velocities (*sensu* Groshens and Orth 1994; Section 3.5.2) between *c.* 0.81 and 1.00 m s^{-1} (Figure 8.1a). Velocities below 0.10 m s^{-1} near the bed were clearly unsuitable. With manipulation of discharges to levels below historical minima, the use by simuliids of a wider middle-range of values, and narrower portion of the upper velocity band than under natural discharges, reflected a patchier availability of high-velocity areas (Figure 8.1a). Although low velocity areas remained prevalent, simuliids showed avoidance of such patches. Comparison of control and impact preference curves showed a marked shift in optimal NBV values from 0.91-1.00 to only 0.51-0.60 at abnormally reduced flows. Concordance between maximum suitability for the flow-impacted utilization and preference curves demonstrated that simuliids were attempting to fully exploit preferred high velocity conditions.

Table 8.5 **Significant Spearman rank order correlations (r_s; P ≤ 0.050) between family abundances and hydraulic habitat variables**. Highly significant results (P ≤ 0.001) are shaded. For each taxon, upper r_s values represent non-transformed abundance data from all sites combined, for natural low flows. Where r_s values were higher for individual sites than for pooled data (only P ≤ 0.001 considered), corresponding site code(s) (E, M, D or R) and r_s are given in parentheses. Lower bold figures in square parentheses represent highly significant results for the data set representing extreme low flows. Taxa in italics showed highly significant biotope specificity at natural low flows. Results for relative exposure are as per relative roughness, but opposite in sign. Ephem. juvs = Ephemeropteran juveniles.

FAMILY / HIGHER TAXON	Depth	Mean column velocity	Near-bed velocity	Froude number	Velocity: depth ratio	Substratum d_{50}	Relative roughness	Turbulence index	Reynolds number	Roughness Reynolds number
Acarina		0.44 (E 0.65) **[0.45]**	0.46 (E 0.65) **[0.46]**	0.44 (E 0.67)	0.44 (E 0.68)		0.12	0.31 (E 0.45)	0.33 (M 0.48)	0.42 (E 0.65)
Cnidaria		0.13	0.11					0.16	0.15	
Dytiscidae							0.11	-0.11	-0.11	
Elmidae		0.42 (R 0.52) **[0.49]**	0.44 (D 0.54) **[0.50]**	0.44 (D 0.54)	0.43 (D 0.55)			0.34 (R 0.52) **[0.49]**	0.33 (R 0.47) **[0.51]**	0.40 (ED 0.51) **[0.45]**
Gyrinidae			0.12			0.17				0.14
Helodidae		0.13	0.12	0.11						0.12
Hydraenidae		0.23	0.25	0.24	0.23	0.12		0.16	0.18	0.25
Collembola	0.19 (D 0.52)	0.19 (D 0.40)	0.15	0.12			-0.16 (D -0.46)	0.27 (D 0.53)	0.27 (D 0.53)	0.13
Blepharoceridae		0.16	0.13	0.14	0.12			0.18 (E 0.34)	0.18 (E 0.32)	0.14
Chironomidae		0.49 (M 0.77) **[0.65]**	0.50 (M 0.77) **[0.65]**	0.49 (M 0.77) **[0.67]**	0.47 (M 0.74) **[0.69]**	(R -0.40)		0.40 (D 0.62) **[0.57]**	0.40 (D 0.63) **[0.56]**	0.45 (M 0.75) **[0.65]**
Empididae		0.25 (D 0.51)	0.25 (D 0.49)	0.23 (D 0.47)	0.20 (D 0.43)			0.21 (D 0.48)	0.22 (D 0.51)	0.22 (D 0.48)
Athericidae		0.31 (D 0.44)	0.31 (D 0.44)	0.31 (D 0.42)	0.30 (D 0.40)	0.13		0.29 (D 0.46)	0.30 (D 0.45)	0.31 (D 0.44)
Simuliidae	-0.16	0.65 (M 0.76) **[0.74]**	0.66 (M 0.77) **[0.77]**	0.66 (M 0.75) **[0.77]**	0.65 (D 0.73) **[0.76]**		0.18	0.50 (R 0.60) **[0.58]**	0.52 (R 0.62) **[0.58]**	0.63 (M 0.72) **[0.73]**
Tipulidae										0.11
Baetidae	-0.14	0.43 (R 0.62) **[0.53]**	0.46 (R 0.62) **[0.59]**	0.45 (R 0.63) **[0.53]**	0.46 (R 0.63) **[0.51]**		0.15	0.28 (R 0.48)	0.29 (R 0.49)	0.44 (R 0.62) **[0.50]**

Table 8.5 Continued.

FAMILY / HIGHER TAXON	Depth	Mean column velocity	Near-bed velocity	Froude number	Velocity: depth ratio	Substratum d_{50}	Relative roughness	Turbulence index	Reynolds number	Roughness Reynolds number
Caenidae		-0.20 (D -0.42)	-0.23 (D -0.46)	-0.22 (D -0.46)	-0.23 (D -0.49)			-0.15	-0.16	-0.23 (D -0.45)
Teloganodidae		-0.16	-0.16	-0.18 (D -0.39)	-0.19 (D -0.42)		(E -0.32)			-0.18 (D -0.39)
Heptageniidae	0.13							0.14 (E 0.34)	0.13	
Ephem. juvs	-0.15						0.17			
Corixidae		-0.21 (E -0.32)	-0.20 (E -0.32)	-0.21	-0.22			-0.20	-0.21	-0.22
Naucoridae	-0.15	-0.13	-0.12	-0.13	-0.13	-0.12	0.13	-0.13	-0.13	-0.13
Notonectidae		-0.21	-0.20	-0.21	-0.21			-0.20	-0.20	-0.21
Veliidae	-0.12						0.13			
Pyraustidae		0.17 (M 0.40)	0.18 (M 0.41)	0.19 (M 0.38)	0.19	0.19	0.14			0.20 (M 0.38)
Corydalidae		0.12	0.12	0.12	0.12					0.13
Nematoda	(D 0.42)	0.23	0.22	0.20	0.18	0.11	(D -0.39)	0.22 (D 0.46)	0.23 (D 0.44)	0.21
Coenagrionidae					-0.11					
Aeschnidae		0.15	0.17	0.15	0.14			0.15	0.14	0.13
Oligochaeta		0.39 (D 0.49)	0.39 (D 0.48)	0.37 (D 0.44)	0.34 (E 0.38)			0.33 (D 0.53)	0.33 (D 0.53)	0.36 (D 0.45)
Platyhelminthes								0.13	0.13	
Notonemouridae	-0.19	(R 0.40)	(R 0.40)	(R 0.45)	0.12 (R 0.47)		0.18 (R 0.40)			(R 0.46)
Glossosomatidae		0.16	0.17	0.17	0.17	0.15				0.21
Hydropsychidae	-0.18	0.53 (E 0.68) **[0.52]**	0.55 (E 0.71) **[0.53]**	0.56 (E 0.72) **[0.46]**	0.56 (E 0.72)	0.23	0.23 (E 0.32)	0.35 (E 0.44)	0.37 (EM 0.45) **[0.44]**	0.57 (E 0.69) **[0.45]**
Hydroptilidae		0.33 (D 0.47)	0.34 (D 0.51)	0.31 (D 0.49)	0.30 (ED 0.48)			0.30 (D 0.43)	0.29 (D 0.43)	0.28 (E 0.47)
Leptoceridae		-0.25 (R -0.47)	-0.26 (R -0.48)	-0.26 (DR -0.48)	-0.25 (R -0.49)			-0.23 (DR -0.41)	-0.22 (R -0.42)	-0.23 (R -0.47)
Philopotamidae		0.29 (EM 0.46)	0.28 (M 0.46)	0.29 (M 0.46)	0.28 (M 0.44)		0.12	0.18	0.18	0.29 (M 0.47)
Polycentropodidae		0.14	0.13	0.14	0.14					0.14
Thripidae									0.11	

Similar patterns of response were observed in relation to Froude number (Figure 8.1b). Under a natural low flow regime, it was clear that simuliids used the most turbulent areas available (particularly Fr > 0.80, with optimum utilization at supercritical flow). In terms of preference, simuliids found areas of very low turbulence (Fr ≤ 0.10) entirely unsuitable, areas with Fr values of 0.11-1.20 marginal, and riffle patches with Fr > 1.20 optimal (Figure 8.1b). At extreme low flows, non-turbulent areas remained unsuitable, with both utilization and preference curves peaking above Fr = 0.90 (Figure 8.1b) as simuliids actively positioned themselves in areas of high turbulence (pers. obs.). The same kinds of trends were anticipated for 0.6V and other velocity-dependent hydraulic parameters that were significantly positively correlated with blackfly densities.

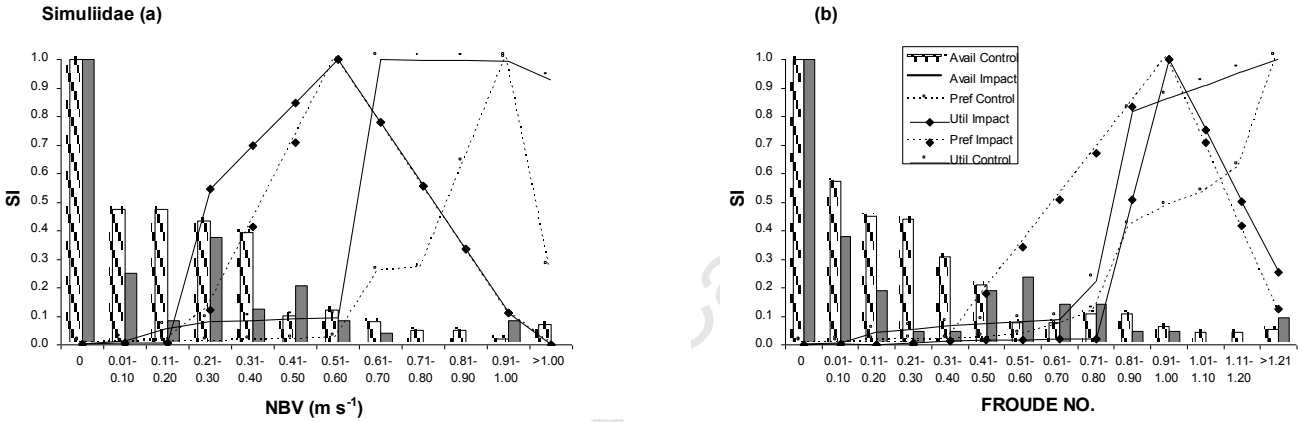


Figure 8.1 Hydraulic habitat availability, utilization and preference for Simuliidae, for (a) near-bottom velocity and (b) Froude number, at natural (control) and extreme (impact) low flows. SI – Suitability Index. Control sample n = 191, Impact sample n = 32.

Unlike the Simuliidae, Leptoceridae exploited a wide range of near-bottom velocities, including maximal use of available slow to non-flowing areas, under natural low flows (Figure 8.2a, control utilization curve). The preference curve revealed optimum NBV values above approx. 0.65 m s^{-1}, while all patches of slower-flowing or standing water were still marginally suitable. With abnormal discharge reduction, there was a slight shift in peak preference from 0.71-0.80 m s^{-1} (natural curve) to the next lowest velocity class. As under natural low flows, however, barely flowing patches were not preferred (Figure 8.2a). For Fr as an index, utilization by leptocerids was higher at conditions of low to zero turbulence, rather than at elevated levels, for both natural and experimental low flows (Figure 8.2b). While both control and impact preference curves indicated a preference for less available patches with higher Fr values, there was a demonstrable shift in optima from > 0.95 (control curve) to 0.21-0.75 with extreme flow reduction (Figure 8.2b).

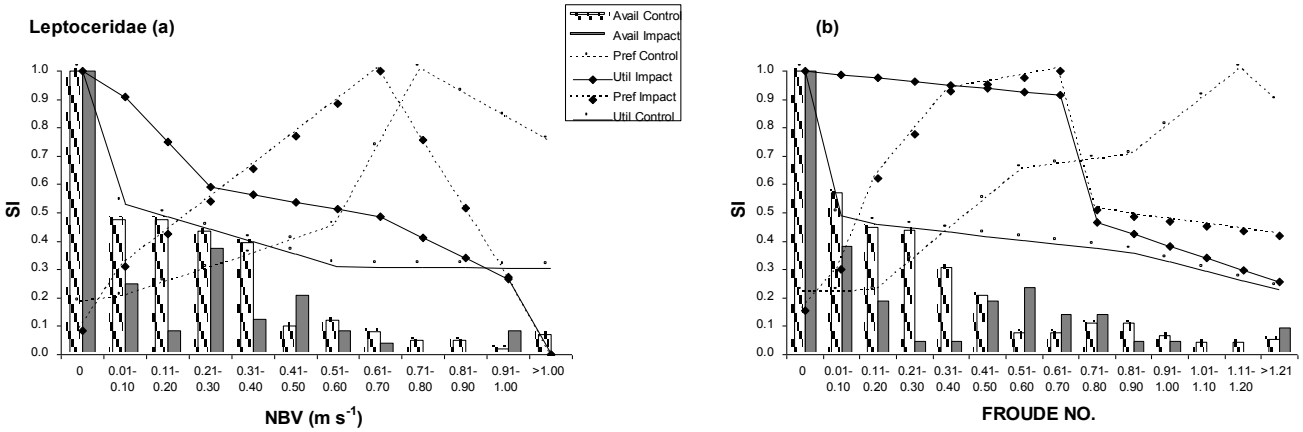


Figure 8.2 Hydraulic habitat availability, utilization and preference for Leptoceridae, for (a) near-bottom velocity and (b) Froude number, at natural (control) and extreme (impact) low flows. Control n = 168, Impact n = 36.

8.4.2 Species hydraulic tolerances at low flows

General relationships at natural low flows

Correlations among chironomid species abundances and hydraulic variables (Table 8.6) generally were of similar strength to those at family level (Section 8.4.1); site-specific relations were not examined, due to relatively low numbers of records for most species. There were significant relationships between abundances and one or more hydraulic factors for 26 species, including all species with highly significant biotope specificities (Table 8.3).

As for family analyses, the weakest species densities-hydraulics correlations were found for depth, as well as relative roughness, RE and substratum d_{50}. Stronger relationships prevailed for velocity and derived indices based in part on depth-velocity interactions, such as Fr. Only *Rheotanytarsus fuscus* showed highly significant positive correlations with all hydraulic indices (i.e. nine out of 11, excluding depth - with which the relationship was negative), supporting its distinct preference for riffles. The strongest relationships with hydraulics, of all species, were apparent for *Notocladius capicola*, the species with greatest riffle specificity. Correlations with population densities attained 0.68, for Fr, 0.6V and NBV (see also below). Other species exhibiting well-developed, positive relationships with most (at least seven) hydraulic variables were *Cricotopus* spp., *Rheocricotopus capensis*, *Thienemanniella lineola*, *Tvetenia calvescens*, and *Conchapelopia trifascia*. Similarly, abundances of *Corynoneura* spp., *Ablabesmyia dusoleili* and *Paramerina* spp. were highly significantly, but negatively correlated with most variables, linked to denser populations in pools.

Table 8.6 **Significant Spearman rank order correlations (r_s; P ≤ 0.050) between chironomid species abundances and hydraulic habitat variables**. Highly significant results (P ≤ 0.001) are shaded. For each species, upper r_s values represent data from all sites in combination, for natural low flows; Lower bold figures in square parentheses represent highly significant results for the data set representing extreme low flows. [BS] - highly significant biotope specificity at natural low flows.

SPECIES / SPECIES GROUP	Depth	Mean column velocity	Near-bed velocity	Froude number	Velocity: depth ratio	Substratum d_{50}	Relative roughness	Turbulence index	Reynolds number	Roughness Reynolds number
Cryptochironomus spp.		-0.19	-0.18	-0.19	-0.19			-0.19	-0.19	-0.19
Polypedilum spp.[BS]		0.20	0.21	0.22	0.22					0.24
Cladotanytarsus spp.	0.14									
Rheotanytarsus fuscus[BS]	-0.20	0.50	0.52	0.52	0.53	0.24	0.27	0.37	0.39	0.54
Tanytarsus spp.						0.15				
Cardiocladius hessei		0.23	0.22	0.22	0.21			0.19	0.20	0.20
Corynoneura spp.	**[0.59]**	-0.28	-0.27	-0.26	-0.23	-0.15	**[-0.57]**	-0.24	-0.26	-0.26
Corynoneura cristata						0.15				
Cricotopus spp.[BS]	-0.16	0.51 **[0.58]**	0.50 **[0.58]**	0.52 **[0.60]**	0.51 **[0.61]**	0.14	0.19	0.43 **[0.48]**	0.44 **[0.46]**	0.50 **[0.53]**
Cricotopus kisantuensis[BS]		0.27 **[0.44]**	0.27 **[0.44]**	0.29	0.28			0.19	0.17	0.24
Cricotopus sp. L						-0.15				
Cricotopus obscurus						0.19				0.16
Eukiefferiella clavigera		0.14		0.16	0.17		0.14			0.17
Nanocladius spp.						-0.18	-0.16			
Notocladius capicola[BS]		0.68 **[0.77]**	0.68 **[0.79]**	0.68 **[0.79]**	0.66 **[0.80]**	0.23	0.17	0.57 **[0.62]**	0.58 **[0.61]**	0.67 **[0.76]**
Parakiefferiella biloba	0.21 **[0.48]**	-0.14	-0.15	-0.16	-0.17	-0.16	-0.23			-0.16
Rheocricotopus capensis[BS]		0.41 **[0.54]**	0.42 **[0.52]**	0.43 **[0.49]**	0.42 **[0.45]**	0.17	0.17	0.32 **[0.52]**	0.33 **[0.52]**	0.42 **[0.44]**
Thienemanniella lineola[BS]		0.44	0.44	0.46	0.47			0.34	0.33	0.45
Thienemanniella trivittata		0.25 **[0.50]**	0.24 **[0.52]**	0.22 **[0.52]**	0.21 **[0.54]**			0.28	0.29	0.21 **[0.53]**

Table 8.6 Continued.

SPECIES / SPECIES GROUP	Depth	Mean column velocity	Near-bed velocity	Froude number	Velocity: depth ratio	Substratum d_{50}	Relative roughness	Turbulence index	Reynolds number	Roughness Reynolds number
Tvetenia calvescens[BS]		0.44	0.46	0.45 **[0.50]**	0.44 **[0.48]**	0.18	0.15	0.35	0.37	0.44 **[0.45]**
Orthoclad sp. A[BS]		0.21	0.22	0.21	0.20			0.21	0.21 **[0.44]**	0.20
Ablabesmyia dusoleili[BS]		-0.40	-0.39	-0.39	-0.40	-0.14		-0.39	-0.39	-0.41
Conchapelopia trifascia[BS]		0.32	0.32	0.31	0.30	0.19		0.27	0.29	0.31
Nilotanypus comatus		0.16	0.14	0.15	0.14			0.16	0.16	
Paramerina spp.[BS]		-0.29	-0.30	-0.29	-0.28			-0.26	-0.27	-0.28
Tanypod juveniles	-0.15	-0.17	-0.20	-0.17	-0.17			-0.18	-0.17	-0.17

Species hydraulic tolerances at extreme low flows

Although overall there remained more chironomid spp. than families with intensified correlations with local hydraulics at very low flows, many chironomids shared the common family loss of highly significant links to microhabitat hydraulics at unnaturally reduced discharges (Table 8.6). All hydraulic variables, other than those weakly influential for the benthos at natural low flows, showed a marked reduction in the number of highly significant relationships at extremely low flows (including, but not restricted to, mean-column velocity, TI, Re and Re_*). Of those chironomid species originally with the highest number of significant correlations at natural flows, almost all no longer showed any highly significant relationships, namely *Rheotanytarsus fuscus*, *Corynoneura* spp., *Thienemanniella lineola*, *Ablabesmyia dusoleili*, *Conchapelopia trifascia* and *Paramerina* spp. In contrast, in a few instances, notably for the riffle indicator, *Notocladius capicola*, there was an intensification of the link to higher velocities and turbulence (to a maximum overall r_s = 0.80, for VD_{ratio}), as such conditions declined in overall availability. *Cricotopus* spp. and *Rheocricotopus capensis* also retained all significant relationships with hydraulic factors at extreme low flows. The same trend did not occur for those species naturally adapted to pool environments, with all three species (viz. *Corynoneura* spp., *Ablabesmyia dusoleili*, *Paramerina* spp.) that showed the highest numbers of highly significant negative relationships with hydraulics showing a decoupling of all such associations when flows became unnaturally low. In a few instances, some relationships with hydraulic conditions only emerged as highly significant for species at very low flows, for example, depth, relative roughness and RE for *Corynoneura* spp., and Reynolds number for Orthoclad sp. A.

Tolerance ranges for hydraulic habitat for indicator chironomid species

Tolerance ranges, based on natural low flow conditions, were determined for select indicator chironomid species and hydraulic variables (Appendix 8.2). Mean tolerance values varied little overall, with the majority of species inhabiting shallow, fairly turbulent microhabitats with moderate to fast velocities (predominantly in riffles); mean and near-bed velocities showed the same patterns. *Cricotopus kisantuensis* exhibited the greatest use of shallow, fast-flowing and turbulent microhabitats. Several other potential indicator species showed similarly high maxima for depth and 0.6V. In contrast, the pool dwelling *Ablabesmyia dusoleili* demonstrated a greater tolerance for deeper (on average), slower-flowing microhabitats without turbulence.

Habitat availability, utilization and preference curves, for natural and extreme low flows, were created for *Notocladius capicola*, the species showing the most distinct preference for riffles in terms of their hydraulic character. Although *N. capicola* used a wide range of near-bed velocities, it was evident that it both maximally utilized and preferred velocities in the order of 0.91-1.00 m s^{-1} (Figure 8.3a). Moreover, current speeds below 0.10 m s^{-1}, though still used in the summer months, were selected against. With extreme flow reduction, *N. capicola* still used a wide range of velocities, but there was a marked shift in peak use, from

that at natural discharges to around 0.21-0.30 m s^{-1} (slow-flowing riffle and run patches), and in greatest preference, to 0.51-0.60 m s^{-1}. For Fr, a similar pattern of utilization and preference was recorded for *N. capicola* under normal low flow conditions (Figure 8.3b). Microhabitats exhibiting Fr figures above *c.* 0.75 were optimal, while entirely non-turbulent areas were unsuitable. The species responded to extremely low flows by shifting its utilization and preference to far lower Fr values than under natural flows, with optima at only 0.31-0.40 (Figure 8.3b). Importantly, as for the other taxa examined, *N. capicola* had restricted scope to express true preference, due to the limited amount of suitable hydraulic habitat available with extreme flow reduction (Chapter 6).

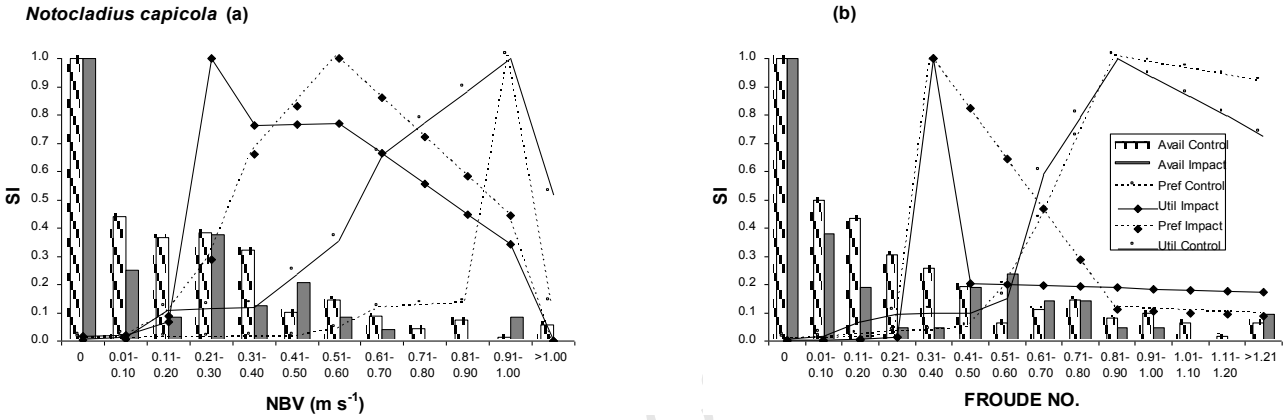


Figure 8.3 Hydraulic habitat availability, utilization and preference for *Notocladius capicola*, for (a) near-bottom velocity and (b) Froude number, at natural (control) and extreme (impact) low flows. Control n = 129, Impact n = 30.

Habitat suitability curves were also generated for *Ablabesmyia dusoleili*, one of the few chironomid species preferring slow-flowing pools (Section 8.3) for which sufficient total numbers of observations were available; analysis was still constrained by the limited observations reflecting artificial flow disturbance. In direct contrast to the invertebrates preferring riffle environments (Figures 8.1 and 8.3), *A. dusoleili* demonstrably preferred pool microhabitats (Figure 8.4). Control patches exhibiting zero to 0.40 m s^{-1} velocities were well utilized, though a preference was shown for values above 0.21 m s^{-1} (Figure 8.4a). Near-bed velocities exceeding 0.40 m s^{-1}, though available were clearly unsuitable for this species in the dry season, with no records of occurrence. Although the same overall pattern was observed with extreme discharge reduction (Figure 8.4a) there appeared to be a reduced preference for standing water. Similarly, both utilization and preference of *A. dusoleili* for turbulent areas at natural low flows declined sharply to nil at Fr > 0.50, though the higher end of the tolerance range was preferred (Figure 8.4b). In the flow-impacted locations, the same pattern was apparent for both SI curves, but with a slight shift in optimum turbulence to higher values than at natural flows (Figure 8.4b).

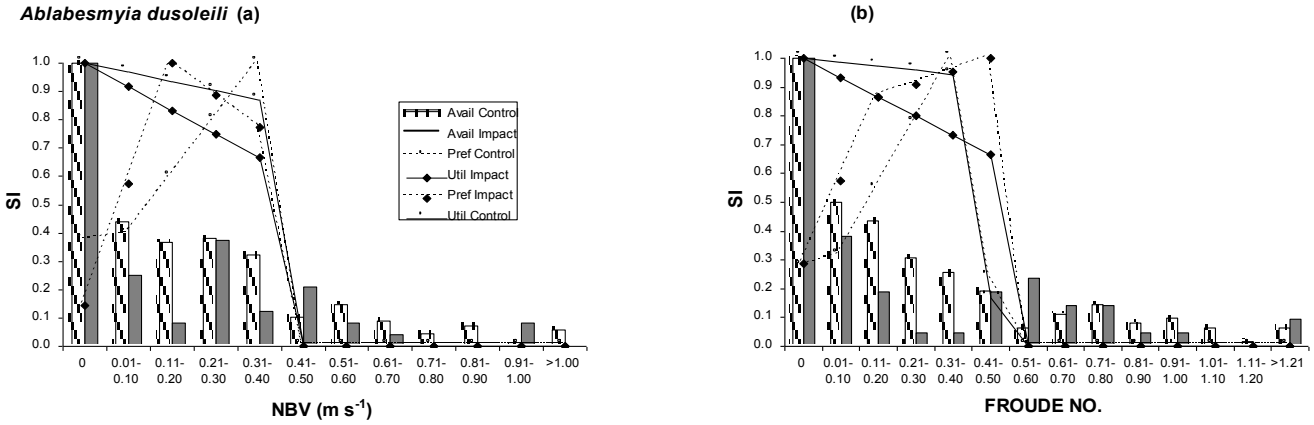


Figure 8.4 Hydraulic habitat availability, utilization and preference for *Ablabesmyia dusoleili*, for (a) near-bottom velocity and (b) Froude number, at natural (control) and extreme (impact) low flows. Control n = 29, Impact n = 11.

8.5 DIRECT DISCHARGE-DIVERSITY RELATIONSHIPS FOR INVERTEBRATES AT LOW FLOWS AND AMONG BIOTOPES

8.5.1 Densities of individual families and discharge reduction

Significant direct relationships with instantaneous discharge were recorded for 19 families across the sites and major biotopes (Table 8.7); there were few instances of non-linearity over the narrow ranges of values examined. Only two relationships were fairly strong, however, namely a positive relationship with discharge for riffle acarinids and a negative one for Notonemouridae in runs, in different rivers. Given the low numbers of observations at species level, as well as the variable results described below for families, similar flow-abundance and other diversity relationships were not assessed for chironomid species.

Under entirely natural low flows, family densities consistently decreased with discharge reduction across riffles and runs, and most strongly for the Philopotamidae and Leptoceridae (Elands site - Table 8.7). No significant results were obtained for pools. At the experimental sites, invertebrate responses occurred in both directions with discharge reduction (Table 8.7). At the Molenaars site, where least flow was diverted, more taxa showed significant changes in abundances with Q_{inst} than with natural levels of flow reduction, whereas for both the severely flow impacted locations, markedly fewer families showed a significant response than under control conditions.

At the Molenaars site, families in riffles responded with increases in numbers as discharge decreased, except in the case of heptageniids. Water mites showed the strongest degree of negative response, but exhibited the opposite trend in runs at the same site. Teloganodids were the only family showing a significant increase in abundance in pools with flow reduction, though exhibiting the converse response in the Riviersonderend R. at even more extremely lowered water levels. At the Du Toits site, the fewest number of significant direct

relationships with discharge were found. Caenids were the only group found in increased densities at lowered discharges in this reach (in runs). In runs and pools at the Riviersonderend site, all significant density-discharge relationships were positive. Increases in abundance as discharge declined were observed for chironomids in riffles, as well as for baetids, when data from all biotopes were pooled.

While oligochaetes and Leptoceridae consistently decreased in abundance with a decrease in flow magnitude, irrespective of site or biotope, several families lacked a consistent response and particularly when compared with trends for the Riviersonderend location. These families included the Acarina, Baetidae, Chironomidae, Caenidae and Teloganodidae.

8.5.2 Relationships between discharge and diversity measures at family level

The nature of relationships between instantaneous discharge and individual diversity indices was explored at family level overall and by biotope type, again focusing on reductions in Q_{inst} magnitude (see also Section 7.6, for a first broader analysis in relation to seasonal flow regime). The results (Tables 8.8-8.17) are discussed separately for each index below.

Relationships between discharge and total number of taxa

It was not possible to establish a consistent regression relationship between Q_{inst} and the total number of families, using data pooled from all sites (natural and extreme low-flows combined) - there was only a slight tendency for taxon numbers to increase with flow reduction (R^2 = 0.05, P = 0.132; Table 8.8). Moreover, examination of rivers individually showed both increases and decreases in the numbers of families with discharge reduction (Table 8.8). The only significant trend, a decrease in S at lower flows, for the Du Toits reach (R^2 = 0.38, P = 0.033), was largely supported by the small numbers (*c.* 10) of families recorded at extremely reduced discharges (Appendix 7.6a).

Although there was no distinct generalised relationship between biotope type and discharge magnitude for runs or pools either, numbers of riffle taxa tended to be higher at lower discharges (Table 8.9). This overall trend and the significant negative relationship observed for the Riviersonderend riffle benthos (R^2 = 0.47, P = 0.014) appeared to be influenced more by very low taxon numbers at the higher discharges experienced in May than by experimental flow treatment(s) (Appendix 7.6a) - high discharges in early summer (December) did not correspond with a similar effect. In the case of the Du Toits, in contrast, the relationship showed a significant decline with discharge reduction to the lowest number of families recorded in riffles at the site, only 3.0, at extreme low flows, as well as the lowest mean (7.3 taxa) (R^2 = 0.42, P = 0.023). For individual sites, run and pool taxa showed weak relationships, of varying direction, with discharge magnitude.

Table 8.7 Significant results ($P \leq 0.050$) for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against individual family abundances (0.1 m^{-2}) overall and for individual biotopes, at each site. Non-significant relationships or data sets with fewer than three cases of non-zero counts were omitted. Individual cases represented mean abundances for individual locations and months (n = 9 replicates).

SITE AND BIOTOPES	n (no. of non-zero counts)	R^2	F	P	TREND (↑ OR ↓) WITH *DECREASE* IN Q
ELANDS					
Biotopes combined					
Oligochaeta	12 (11)	0.338	5.097	0.048	↓
Glossosomatidae	12 (4)	0.376	6.028	0.034	↓
Philopotamidae	12 (11)	0.387	6.323	0.031	↓
Riffles					
Oligochaeta	12 (9)	0.354	5.475	0.041	↓
Leptoceridae	12 (4)	0.395	6.531	0.029	↓
Philopotamidae	12 (10)	0.361	5.659	0.039	↓
Runs					
Simuliidae	12 (6)	0.371	5.910	0.035	↓
Philopotamidae	12 (3)	0.413	7.034	0.024	↓
Pools					
None	-	-	-	-	-
MOLENAARS					
Biotopes combined					
Ceratopogonidae	12 (11)	0.349	5.350	0.043	↑
Pyraustidae	12 (7)	0.356	5.527	0.041	↑
Riffles					
Acarina	12 (12)	0.552	12.328	0.006	↑
Elmidae	12 (11)	0.409	6.918	0.025	↑
Limnichidae	12 (7)	0.346	5.301	0.044	↑
Heptageniidae	12 (12)	0.415	7.092	0.024	↓
Pyraustidae	12 (7)	0.356	5.527	0.041	↑
Runs					
Acarina	12 (11)	0.364	5.721	0.038	↓
Baetidae	12 (12)	0.439	7.815	0.019	↓
Pools					
Chironomidae	12 (12)	0.347	5.302	0.044	↓
Caenidae	12 (4)	0.354	5.483	0.041	↓
Teloganodidae	12 (11)	0.495	9.820	0.011	↑
DU TOITS					
Biotopes combined					
Hydraenidae	12 (9)	0.360	5.619	0.039	↓
Riffles					
Leptophlebiidae	12 (9)	0.343	5.225	0.045	↓
Leptoceridae	12 (11)	0.359	5.595	0.040	↓
Runs					
Caenidae	12 (8)	0.346	5.301	0.044	↑
Pools					
None	-	-	-	-	-

Table 8.7 Continued.

SITE AND BIOTOPES	n (no. of non-zero counts)	R^2	F	*P*	TREND (↑ OR ↓) WITH *DECREASE* IN Q
RIVIERSONDEREND					
Biotopes combined					
Baetidae	12 (12)	0.351	5.411	0.042	↑
Riffles					
Chironomidae	12 (12)	0.397	6.593	0.028	↑
Runs					
Notonemouridae	12 (3)	0.508	10.319	0.009	↓
Pools					
Teloganodidae	12 (12)	0.391	6.417	0.030	↓
Oligochaeta	12 (6)	0.454	8.311	0.016	↓
Hydroptilidae	12 (8)	0.376	6.034	0.034	↓

Table 8.8 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against total number of families (*S*, 0.1 m^{-2}). Where data from different sites were pooled, Q was normalised by Q_{50}, and numbers of taxa were expressed as a function of site maxima. ^{T} indicates log transformation. Shading indicates significance at $P \leq 0.050$. n - number of samples; R^2 - coefficient of determination.

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
All sites combined	48	0.049	2.352	0.132	↑
Elands ^{T}	12	0.154	1.823	0.207	↓
Molenaars ^{T}	12	0.101	1.127	0.313	↑
Du Toits ^{T}	12	0.378	6.083	0.033	↓
Riviersonderend ^{T}	12	0.293	4.146	0.069	↑

Effects of discharge magnitude on numbers of individuals

Overall, there was only a weakly negative relationship between instantaneous discharge and invertebrate abundances ($R^2 = 0.052$, $P = 0.121$; Table 8.10) and no consistent or significant trends emerged either for individual sites (Table 8.10). At the Du Toits, although numbers of individuals typically increased with a decrease in discharge, variability in numbers was marked with both extremely high and low abundances encountered at lowest flows (Feb: $\bar{x} = 1482.6 \pm 2366.4$ 0.1 m^{-2} cf. Mar: $\bar{x} = 656.0 \pm 535.9$ 0.1 m^{-2}). In the case of the Riviersonderend, a slightly stronger negative relationship between Q_{inst} and overall abundance was found.

Regression analysis revealed a weak, but significant increase in the total number of individuals inhabiting riffles at lower discharges ($R^2 = 0.111$, $P = 0.021$; Table 8.11). The relationship was the only clear generalisation possible across all sites, for any diversity index. However, individual sites showed differential invertebrate responses within riffles, as well as other biotope types (Table 8.11). The sole significant,

negative relationship was found for the Riviersonderend site ($R^2 = 0.551$, $P = 0.006$). Most notably, under an entirely natural flow regime (Elands control site) riffle fauna exhibited an inverse relationship to the overall one also shown by the Riviersonderend site. Inconsistent relationships between numbers of individuals and discharge were found for run assemblages. Furthermore, the overall relationship was only weakly negative, as was that of riffle fauna. Pool assemblages showed either no response or a decline in total numbers of individuals with discharge reduction.

Table 8.9 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against total number of families (*S*, 0.1 m^{-2}) for biotopes at individual sites.

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
Riffles					
All sites combined	48	0.045	2.153	0.149	↑
EL	12	0.144	1.686	0.223	↓
MO	12	0.114	1.293	0.282	↑
DU [T]	12	0.420	7.252	0.023	↓
RI [T]	12	0.468	8.808	0.014	↑
Runs					
All sites combined	48	0.0004	0.017	0.897	none
EL [T]	12	0.061	0.651	0.439	↓
MO	12	0.013	0.129	0.727	↑
DU	12	0.115	1.301	0.281	↓
RI	12	0.002	0.016	0.903	none
Pools					
All sites combined	48	0.0002	0.009	0.926	none
EL [T]	12	0.033	0.343	0.571	↓
MO [T]	12	0.0005	0.005	0.946	none
DU [T]	12	0.010	0.105	0.753	↑
RI [T]	12	0.022	0.220	0.649	↑

Table 8.10 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against total number of individuals (*N*, 0.1 m^{-2}).

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
All sites combined	48	0.052	2.501	0.121	↑
Elands [T]	12	0.198	2.467	0.147	↓
Molenaars [T]	12	0.132	1.518	0.246	↓
Du Toits	12	0.194	2.413	0.151	↑
Riviersonderend [T]	12	0.316	4.611	0.057	↑

Table 8.11 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against total number of individuals (*N*, 0.1 m^{-2}) for biotopes at individual sites.

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
Riffles					
All sites combined	48	0.111	5.727	0.021	↑
EL	12	0.085	0.929	0.358	↓
MO [T]	12	0.026	0.263	0.619	↓
DU	12	0.179	2.179	0.171	↑
RI [T]	12	0.551	12.285	0.006	↑
Runs					
All sites combined	48	0.016	0.769	0.385	↑
EL [T]	12	0.207	2.603	0.138	↓
MO [T]	12	0.284	3.960	0.075	↓
DU [T]	12	0.099	1.104	0.318	↑
RI	12	0.197	2.446	0.149	↑
Pools					
All sites combined	48	0.001	0.053	0.819	none
EL	12	0.068	0.726	0.414	↓
MO	12	0.225	2.907	0.119	↓
DU [T]	12	0.002	0.018	0.895	none
RI	12	0.007	0.073	0.793	none

Responses in family richness to discharge reduction

Regression relationships between family richness and flow magnitude were weak, and inconsistent in response direction, for all sites combined, as well as for the Molenaars, Riviersonderend and Elands reaches (Table 8.12). The singular significant trend, a decrease in richness with decreasing discharge, was found at the Du Toits site ($R^2 = 0.42$, $P = 0.023$).

Table 8.12 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against family richness (Margalef's index, *d*) (0.1 m^{-2}).

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
All sites combined	48	0.018	0.828	0.368	↑
Elands [T]	12	0.070	0.752	0.406	↓
Molenaars [T]	12	0.175	2.114	0.177	↑
Du Toits [T]	12	0.417	7.148	0.023	↓
Riviersonderend	12	0.043	0.449	0.518	↑

Examination of richness for specific biotopes in relation to discharge magnitude (Table 8.13) revealed no significant general trends across all sites. For riffles in particular, trends lacked consistency among sites, with the strongest, converse relationships recorded for one of the two sites at which most flow was diverted -

the Du Toits site (R^2 = 0.39, P = 0.030). For runs and especially pools, there were no significant dependencies of richness on discharge magnitude.

Table 8.13 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against family richness (d, 0.1 m^{-2}) for biotopes at individual sites.

SITE	n	R^2	F	P	TREND WITH *DECREASE* IN Q
Riffles					
All sites combined	48	0.021	0.992	0.325	↑
EL	12	0.096	1.064	0.327	↓
MO	12	0.089	0.980	0.346	↑
DU [T]	12	0.390	6.401	0.030	↓
RI [T]	12	0.258	3.476	0.092	↑
Runs					
All sites combined	48	0.020	0.920	0.343	↓
EL [T]	12	0.003	0.032	0.862	none
MO [T]	12	0.254	3.409	0.095	↑
DU [T]	12	0.300	4.284	0.065	↓
RI [T]	12	0.066	0.708	0.420	↓
Pools					
All sites combined	48	0.001	0.048	0.828	none
EL [T]	12	0.006	0.059	0.812	none
MO [T]	12	0.014	0.142	0.714	↑
DU [T]	12	0.023	0.240	0.635	↑
RI [T]	12	0.015	0.156	0.701	↑

Relationships between assemblage evenness and discharge

For all sites in combination, there was no relationship between evenness and Q_{inst} (Table 8.14). In most instances, however, there was an increase in taxon equitability with discharge reduction at site level (Table 8.14), a dependency that was most pronounced for the Molenaars reach (R^2 = 0.58, P = 0.004). A converse, but relatively weak relationship was found for the Riviersonderend site.

Table 8.14 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against Pielou's evenness index (J') (0.1 m^{-2}).

SITE	n	R^2	F	P	TREND WITH *DECREASE* IN Q
All sites combined	48	0.009	0.412	0.524	none
Elands [T]	12	0.271	3.716	0.083	↑
Molenaars	12	0.582	13.930	0.004	↑
Du Toits [T]	12	0.021	0.218	0.651	↑
Riviersonderend	12	0.179	2.183	0.170	↓

While overall assemblage evenness tended to decrease in riffles and increase in pools with discharge reduction, there was no apparent trend for runs (Table 8.15). Both increases (significant in the Molenaars case: $R^2 = 0.54$, $P = 0.007$) and decreases in the evenness of riffle assemblages were observed for individual sites. For both sites at which extreme flow reduction occurred the Q-J' trend was positive, and highly significantly so in the case of the Riviersonderend ($R^2 = 0.70$, $P < 0.001$). Except for the Riviersonderend, run assemblages at the sites showed increased equitability across families as discharge declined. However, the relationship was only significantly strong at the Molenaars site ($R^2 = 0.45$, $P = 0.017$). The observed general relationship for pools held at site level, although no trend was apparent for the Riviersonderend.

Table 8.15 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against evenness (*J'*, *0.*1 m^{-2}) for biotopes at individual sites.

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
Riffles					
All sites combined	48	0.045	2.181	0.147	↓
EL [T]	12	0.138	1.608	0.234	↑
MO	12	0.536	11.529	0.007	↑
DU [T]	12	0.156	1.852	0.203	↓
RI	12	0.699	23.242	0.0007	↓
Runs					
All sites combined	48	0.004	0.120	0.657	none
EL [T]	12	0.256	3.439	0.093	↑
MO	12	0.450	8.193	0.017	↑
DU	12	0.035	0.365	0.559	↑
RI [T]	12	0.085	0.934	0.357	↓
Pools					
All sites combined	48	0.032	1.501	0.227	↑
EL [T]	12	0.053	0.555	0.473	↑
MO [T]	12	0.129	1.486	0.251	↑
DU [T]	12	0.098	1.080	0.323	↑
RI	12	0.006	0.062	0.808	none

Relationships between assemblage diversity and discharge

Table 8.16 provides the results of linear regression of Shannon-Wiener diversity, H', against discharge at site level. In general, and for two of the sites (those of greatest diversions), no dependency of diversity on discharge magnitude was found. In the other two cases, the relation was negative, and significantly so for the Molenaars reach both overall ($R^2 = 0.53$, $P = 0.007$; Table 8.16) and for separate biotopes (Table 8.17).

Individual treatment of relationships by biotope type showed differing trends in assemblage diversity with declining discharge (Table 8.17). For each of the experimental sites, a different response in riffle diversity

was recorded. While the Molenaars showed a similar, but far stronger increase in diversity with flow reduction (R^2 = 0.53, P = 0.008) than the control site, the Du Toits exhibited a lesser but significant decrease (R^2 = 0.38, P = 0.033). In most instances, there was an increase in diversity with decreasing discharge for run assemblages, most pronounced in the Molenaars reach (R^2 = 0.49, P = 0.011). The Riviersonderend weakly showed the opposite response, with a decrease in run faunal diversity with a decline in discharge, the sole biotope-specific trend for the site. Consistent, but very weakly negative Q-H' relationships were found for pool assemblages.

Table 8.16 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against Shannon-Wiener diversity (*H'*) at family level (0.1 m^{-2}).

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
All sites combined	48	0.0005	0.023	0.880	none
Elands	12	0.162	1.930	0.195	↑
Molenaars	12	0.532	11.375	0.007	↑
Du Toits	12	0.005	0.047	0.834	none
Riviersonderend	12	0.009	0.088	0.773	none

Table 8.17 Results for regression of discharge (Q_{inst}, $m^3 s^{-1}$) against family-level diversity (*H'*, 0.1 m^{-2}) for biotopes at individual sites.

SITE	n	R^2	F	*P*	TREND WITH *DECREASE* IN Q
Riffles					
All sites combined	48	0.032	1.509	0.226	↓
EL	12	0.068	0.735	0.411	↑
MO	12	0.526	11.078	0.008	↑
DU	12	0.380	6.132	0.033	↓
RI	12	0.002	0.019	0.892	none
Runs					
All sites combined	48	0.00001	0.0005	0.982	none
EL	12	0.148	1.743	0.216	↑
MO	12	0.491	9.640	0.011	↑
DU	12	0.011	0.109	0.748	↑
RI	12	0.064	0.680	0.429	↓
Pools					
All sites combined	48	0.014	0.675	0.416	↑
EL	12	0.021	0.217	0.651	↑
MO	12	0.049	0.520	0.487	↑
DU	12	0.161	1.923	0.196	↑
RI	12	0.009	0.087	0.774	none

Within-site trends in relationships between diversity indices and discharge

Although there were few consistent trends with discharge reduction by index or biotope across sites, within each site there was a greater consistency in at least the response direction (sign) per diversity index (comparisons of above overall results with corresponding biotope-specific results; Tables 8.8-8.17).

Under an entirely natural low flow regime (Elands), both the number of families and the numbers of individuals decreased with discharge reduction (also reflected in a decrease in *d*). There was a concomitant increase in evenness (and hence, decline in the dominance of individual families) and Shannon-Wiener diversity; the pattern was the same across all biotopes. Similar trends were observed for the Molenaars site, for all variables except family number and richness, both of which increased with a decline in discharge. As occurred at the Elands site, the general pattern held across riffles, runs and pools, for all indices examined. At the Du Toits site, there was a mixed response with some effects matching those of the control site, while total numbers of invertebrates increased and taxon dominance decreased at lower flows. Most notably, however, the overall trend broke down when examined for individual biotopes. In particular, both equitability and diversity decreased in riffles as discharge decreased, while correspondingly increasing in runs and pools. Within pools, there were also increases in the numbers of taxa present and richness with flow reduction. Interestingly, overall, the Riviersonderend site showed the opposite trends to that of the control site for all four indices for which a trend was apparent. In marked contrast with all other sites also was an increase in family-level dominance with flow reduction. Where they existed, trends were maintained for riffles and pools. However, run assemblages demonstrated decreases in richness and H' at the lower end of the spectrum of discharges encountered.

The shifts in trends in diversity indices among biotopes for the sites that included flow-impacted assemblages, perhaps more so than overall trends relative to the control site, indicated a possible, interactive influence of extreme low flows on inter-biotope diversity.

8.6 INTERRELATIONSHIPS BETWEEN INVERTEBRATE ASSEMBLAGE COMPOSITION AND ABIOTIC MEASURES OF LOW-FLOW DISTURBANCE

8.6.1 Relating assemblage response to changes in habitat quality at low flows

The extent to which the patterns of similarity among invertebrate assemblages from different biotopes across locations and sites (Section 7.4, Figures 7.2b-7.5b) could be explained by solely habitat hydraulic quality at low flows is indicated in Table 8.18. Similar analyses could not be performed for other ecological descriptors of habitat, including chemistry, due to data limitations at this scale.

Table 8.18 Results of BIOENV analyses of combinations of hydraulic habitat variables yielding the best matches with benthic macroinvertebrate assemblages at each site (mean family abundances per biotope at control and impact locations) over the full dry season, based on Spearman rank correlation (ρ) *k* number of variables at a time. k ≤ 5 variables required for best fit in bold italics. ρ_s rounded to 2 decimal places.

	SITE AND BEST VARIABLE COMBINATIONS (ρ)			
k	**EL**	**MO**	**DU**	**RI**
1	***Fr*** ***(0.44)***	0.6V (0.57)	Fr (0.46)	Fr (0.24)
2	Fr, VD_{ratio} (0.43)	0.6V, RE (0.57)	***Fr, R_{rel}*** ***(0.61)***	D, Fr (0.28)
3	NBV, Fr, VD_{ratio} (0.43)	0.6V, NBV, R_{rel} (0.59)	NBV, Fr, R_{rel} (0.61)	D, Fr, $SUBd_{50}$ (0.30)
4	NBV, Fr, VD_{ratio}, Re_* (0.42)	0.6V, NBV, R_{rel}, RE (0.61)	0.6V, NBV, Fr, R_{rel} (0.60)	***D, 0.6V, Fr, $SUBd_{50}$*** ***(0.31)***
5	0.6V, NBV, Fr, VD_{ratio}, Re_* (0.41)	***0.6V, NBV, R_{rel}, RE, Re_**** ***(0.61)***	0.6V, NBV, Fr, VD_{ratio}, R_{rel} (0.59)	D, 0.6V, Fr, $SUBd_{50}$, Re_* (0.30)

Abbreviations (Section 3.4.4): D - depth; NBV - near bottom velocity; 0.6V - mean column velocity; Fr - Froude number; VD_{ratio} - velocity: depth ratio; Re_* - roughness Reynolds number; R_{rel} - relative roughness; RE - relative exposure; TI - turbulence index; $SUBd_{50}$ - substratum median particle size.

There was a low match between hydraulic variables and the differentiation of assemblages for the Elands, moderate correlations for the Molenaars and Du Toits, and a very weak match for the Riviersonderend site. In the Riviersonderend R., water depth and substratum appeared more influential aspects of habitat than in the other reaches. One to five hydraulic habitat variables sufficed to indicate separation by biotope type, with little increase in the strength of relationships as additional hydraulic variables were added. Supporting previous analyses, Fr was a key variable, representing the best single-variable discriminator for three of the sites, with VD_{ratio} having a similar influence. Near-bottom and mean column velocity also exerted effects on assemblage composition.

An analysis focused on the peak low-flow period also demonstrated that the quality of hydraulic habitat alone weakly explained the separation of invertebrate assemblages in ordination space (see Section 7.4, ordination plots of Figures 7.6-7.9), with low to moderate correlations for all sites (Table 8.19). The best-fit result was obtained for the Molenaars site (ρ = 0.50), which also showed strong hydraulic biotope differentiation at low flows (Section 6.4). The most influential variables included mean column and near-bottom velocities, Fr and VD_{ratio} and, particularly for flow impacted sites, relative roughness. Different, though often closely related, variables were implicated in the differentiation of assemblages at the sites. A maximum of five microhabitat variables influenced the separation of assemblages based on general biotope character, especially at pool-riffle extremes and in relation to outliers. It did not, however, provide the level of resolution required to understand finer assemblage groupings. This was true for the flow-impacted assemblages, where inconsistencies were in part due to widely differing hydraulic quality across the flow-

disturbed samples. These findings were verified by bubble plots, where the magnitudes of each of the best-fit hydraulic variables were superimposed separately on samples for each ordination plot.

Table 8.19 Results of BIOENV analyses of combinations of hydraulic habitat variables yielding the best matches with benthic macroinvertebrate assemblages at each site during the flow impact phase, based on Spearman rank correlation (ρ) *k* number of variables at a time. Assemblages were examined at the level of individual samples within major biotopes. k ≤ 5 variables required for best fit in bold italics.

	SITE AND BEST VARIABLE COMBINATIONS (ρ)			
k	**EL**	**MO**	**DU**	**RI**
1	Re_* (0.36)	NBV (0.43)	VD_{ratio} (0.29)	0.6V (0.27)
2	RE, Re_* (0.40)	NBV, R_{rel} (0.47)	VD_{ratio}, R_{rel} (0.30)	***0.6V, R_{rel}*** ***(0.40)***
3	***0.6V, RE, Re_**** ***(0.44)***	***0.6V, NBV, R_{rel}*** ***(0.50)***	Fr, VD_{ratio}, R_{rel} (0.31)	0.6V, NBV, R_{rel} (0.39)
4	0.6V, Fr, RE, Re_* (0.43)	0.6V, NBV, Fr, R_{rel} (0.48)	NBV, Fr, VD_{ratio}, R_{rel} (0.31)	0.6V, NBV, Fr, R_{rel} (0.38)
5	0.6V, Fr, $SUBd_{50}$, RE, Re_* (0.44)	0.6V, NBV, Fr, R_{rel}, TI (0.47)	***0.6V, NBV, Fr, VD_{ratio}, R_{rel}*** ***(0.32)***	0.6V, NBV, Fr, $SUBd_{50}$, R_{rel} (0.37)

Abbreviations (Section 3.4.4): NBV - near bottom velocity; 0.6V - mean column velocity; Fr - Froude number; VD_{ratio} - velocity: depth ratio; Re_* - roughness Reynolds number; R_{rel} - relative roughness; RE - relative exposure; TI - turbulence index; $SUBd_{50}$ - substratum median particle size.

8.6.2 Interrelationships between invertebrate diversity and flow-mediated abiotic conditions

The above results pointed to the need to incorporate measures of physical habitat quantity alongside hydraulic quality, as well as other variables reflecting potential abiotic change, including water quality variables (Chapter 5) and descriptors of instantaneous flow, to better characterize low flows. Also, the previous findings suggested that simpler measures of invertebrate assemblage composition might yield improved outcomes. The results, for each site, of multiple regressions of diversity indices for riffle assemblages, against a full array of such abiotic variables are presented in Table 8.20, with highly inter-correlated variables excluded; other biotopes were not examined, due to the limited interpretation possible.

Significant interrelationships were identifiable for riffle diversity on the basis of physical habitat quantity and quality (as described by discharge, patch characteristics and microhabitat hydraulics), water chemistry, and both sets of variables in combination, though with a range of variables implicated across the different diversity measures and rivers. Relationships were weakest for the control site, whereas flow impacted sites, particularly the Riviersonderend River, exhibited several highly significant and strong relations. In the majority of cases, best-fit regression relationships were obtained for invertebrate diversity measures when both physical habitat and chemistry factors were included, especially for the Molenaars site, where this was

true for all analyses (Table 8.20). For the Elands, it was only for species richness that dry-season water quality assumed greater significance than habitat and chemistry combined. For the two most flow altered locations, physical habitat was more influential than under control conditions (Elands) in structuring assemblage diversity (recognising that data from both control and impact locations were included for experimental sites). This effect was most notable for taxon richness in the Du Toits reach, and richness and abundance in the Riviersonderend R.

Across the rivers, the physical habitat variables commonly influencing diversity were the wetted surface area, width and perimeter of riffles, as well as the hydraulic variables VD_{ratio}, RE, water depth, NBV and Fr (Table 8.20). A further 12 habitat variables were also of some influence. Of the 15 chemical variables related with biotic diversity, conductivity was most commonly influential (Table 8.20), lending support to earlier observations of a relationship between discharge reduction and EC (Section 5.3). The concentrations of silicon, total nitrogen, sulphate, and dissolved oxygen in riffle patches (%OxBio) were also often significantly associated with the different diversity indices. In a few instances, the best-fit regression relationship with a diversity index was found for a single physical habitat or biotope-specific chemical variable, namely VD_{ratio}, RE, depth, instantaneous discharge (as a flow percentile), or %OxBio.

8.6.3 Interrelationships among indicator taxa and flow-related changes in physical habitat and chemistry

Although significant and strong relationships between densities and physical habitat (including flow), chemistry, or both sets of variables were found, there was a lack of consistency across sites and combinations of variables for the indicator taxa, Simuliidae, *Notocladius capicola* and *Ablabesmyia dusoleili* (Table 8.21). Leptoceridae were excluded from analyses, as they did not show a marked biotope preference (Section 8.3).

8.7 INVERTEBRATE RESPONSES TO LOW-FLOW DISTURBANCE HISTORY: LINKS TO KEY FLOW INDICES

The above analyses largely established the extent to which response to low flows could be characterized for individual invertebrate taxa or measures of assemblage diversity on the basis of changes in physical habitat at biotope scale, chemistry, and the magnitude of instantaneous discharge (on the day of sampling). In this section, any connections between invertebrate assemblage response and the longer-term, low-flow disturbance history of the sites are made explicit, using only natural flow data sets. Reference is made to river monthly and annual flow characteristics, as established in Chapter 4 (in particular, Section 4.4; see also Figure 4.10 and Table 4.9).

Table 8.20 Results for forward, stepwise multiple regression of assemblage diversity indices against physical habitat (including discharge) and water chemistry variables, for riffle biotopes at each site. Control and impact data were treated separately across all study months with mean values calculated per location and month. Only the best-fit relationships are presented (* - different combinations of variables generated a similar result). Highly significant results ($P \leq 0.001$) are shaded. NS - not significant. See footnote for abbreviations for variables.

SITE	EL				MO				DU				RI			
DIVERSITY INDEX	**F (n, df)**	***P***	***R^2***	***var(s)***	**F (n, df)**	***P***	***R^2***	***var(s)***	**F (n, df)**	***P***	***R^2***	***var(s)***	**F (n, df)**	***P***	***R^2***	***var(s)***
Number of taxa (*S*)																
Habitat	-	NS	-	-	(1, 10) = 21.207	0.001	0.68	RE	(5, 6) = 16.512	0.002	0.88	* D, RE, WW-Bio, %flow, Tr%Wet	(4, 7) = 28.982	0.000	0.91	Re*, WPBio, Pat-BioSA, Fr
Chemistry	-	NS	-	-	(4, 7) = 13.730	0.002	0.82	EC, Si, Ca, T_{min}	(5, 6) = 14.486	0.003	0.86	* EC, %OxBio, Cl, PO_4, TotN	(5, 6) = 11.607	0.005	0.83	%OxBio, Si, EC, TotN, pH
Both	(5, 6) = 8.385	0.011	0.77	R_{rel}, Pat-%Bio, WW-Bio, Ca, TotN	(7, 4) = 33.887	0.002	0.95	* RE, SO_4, TotN, PO_4, R_{rel}, EC, TI	(6, 5) = 17.685	0.003	0.90	* D, RE, WW-Bio, %OxBio, %flow, Tr%Wet	(3, 8) = 48.131	0.000	0.93	* %OxBio, Pat-BioSA, Fr
Number of individuals (*N*)																
Habitat	(1, 10) = 12.075	0.006	0.55	VD_{ratio}	(3, 8) = 5.255	0.027	0.54	$SUBd_{50}$, VD_{ratio}, WPBio	(1, 10) = 6.965	0.025	0.41	VD_{ratio}	(6, 5) = 187.110	0.000	0.99	Tr%Wet, D, %flow, WPBio, Pat-BioSA, Q_{inst}
Chemistry	(2, 9) = 15.832	0.001	0.73	Ca, NO_2	(6, 5) = 9.211	0.014	0.82	Si, TotN, %OxBio, PO_4, SO_4, EC	(4, 7) = 4.436	0.042	0.56	Alk, Cl, TotN, EC	(4, 7) = 12.178	0.003	0.80	SO_4, Alk, Si, T_{max}
Both	(2, 9) = 21.393	0.000	0.79	NO_2, R_{rel}	(5, 6) = 34.895	0.000	0.94	* Fr, VD_{ratio}, $SUBd_{50}$, TotN, Si	(3, 8) = 30.525	0.000	0.89	* Fr, Alk, Cl	(6, 5) = 16.107	0.004	0.89	Tr%Wet, SO_4, WP-Bio, %flow, Alk, D

Table 8.20 Continued.

SITE	EL				MO				DU				RI			
DIVERSITY INDEX	F (n, df)	*P*	R^2	*var(s)*	F (n, df)	*P*	R^2	*var(s)*	F (n, df)	*P*	R^2	*var(s)*	F (n, df)	*P*	R^2	*var(s)*
Species richness (*d*)																
Habitat	-	NS	-	-	(1, 10) = 11.156	0.007	0.53	D	(8, 3) = 31.965	0.008	0.96	D, RE, WW-Bio, NoCh, NBV, Re*, R_{rel}, d≤0.05%	(3, 8) = 19.860	0.000	0.84	Re*, NBV, Tr%Bio
Chemistry	(5, 6) = 10.705	0.006	0.82	Cl, PO_4, Alk, Mg, NO_2	(5, 6) = 5.676	0.028	0.68	EC, Si, Ca, TotN, %OxBio	-	NS	-	-	(1, 10) = 14.392	0.004	0.59	%OxBio
Both	(3, 8) = 4.342	0.043	0.48	Pat-BioSA, Cl, PO_4	(9, 2) = 150.32	0.007	0.99	D, Si, EC, R_{rel}, RE, NBV, %OxBio, Ca, SO_4	(4, 7) = 8.867	0.007	0.74	D, RE, WW-Bio, %OxBio	as per Habitat	as per Habitat	as per Habitat	as per Habitat
Evenness (*J'*)																
Habitat	(3, 8) = 4.942	0.031	0.52	Tr%Bio, WW-Bio, Q_{inst}	(1, 10) = 18.925	0.001	0.65	Q%	(4, 7) = 8.872	0.007	0.74	* VD_{ratio}, WP-Bio, NoCh, Fr	(3, 8) = 41.973	0.000	0.92	* Pat-BioSA, RE, WW-Bio
Chemistry	(3, 8) = 4.805	0.034	0.51	Ca, NO_2, EC	(3, 8) = 7.223	0.012	0.63	EC, Si, TotN	(4, 7) = 5.129	0.030	0.60	Cl, SO_4, EC, TBio	(6, 5) = 42.751	0.000	0.96	Alk, SO_4, pH, %OxBio, Si, Mg
Both	(6, 5) = 10.692	0.010	0.84	Ca, d≤0.05%, Pat-BioSA, NO_2, WP-Bio, $SUBd_{50}$	(4, 7) = 74.432	0.000	0.96	* Q%, WW-Bio, TotN, Si	(5, 6) = 24.056	0.001	0.91	VD_{ratio}, Cl, SO_4, TotN, WP-Bio	(5, 6) = 140.890	0.000	0.98	* Alk, WW-Bio, %OxBio, Pat-BioSA, RE
Diversity (*H'*)																
Habitat	(2, 9) = 4.630	0.041	0.40	WW-Bio, Pat-%Bio	(2, 9) = 9.498	0.006	0.61	Q%, VD_{ratio}	(2, 9) = 19.457	0.001	0.77	VD_{ratio}, Fr	(3, 8) = 15.258	0.001	0.80	* NBV, WW-Bio, NoCh
Chemistry	(4, 7) = 5.073	0.031	0.60	Si, PO_4, SO_4, Alk	(3, 8) = 14.125	0.001	0.78	EC, Si, TotN	(4, 7) = 8.106	0.009	0.72	* Cl, EC, SO_4, PO_4	-	NS	-	-
Both	(6, 5) = 12.069	0.008	0.86	* Si, PO_4, SO_4, Alk, WW-Bio, VD_{ratio}	(4, 7) = 38.450	0.000	0.93	* Tr%Wet, EC, TotN, Si	(6, 5) = 137.830	0.000	0.99	* VD_{ratio}, Cl, EC, %flow, SO_4, PO_4	(5, 6) = 13.130	0.004	0.85	NBV, WW-Bio, NoCh, SO_4, TBio

Variables: Fr - Froude number; VD_{ratio} - velocity: depth ratio; NBV - near-bed velocity; TI - turbulence index; R_{rel} - Relative roughness; RE - relative exposure; D - water depth; d≤0.05% - water depth ≤ 0.05 m; Re* - Roughness Reynolds number; WPBio - riffle wetted perimeter; WW-Bio - riffle transect wetted width ; Pat-BioSA - riffle patch surface area ; %flow - % flowing water; Tr%Bio - proportion of cross-section as riffle as %; NoCh - number of channels; Tr%Wet - transect total wetted width as %; $SUBd_{50}$ - substratum median particle size; Q_{inst} - instantaneous discharge; Q% - Q_{inst} percentile on FDC; EC - conductivity; Ca - Calcium; Cl - Chloride; TotN - nitrate and nitrite combined; NO_2 - Nitrite; PO_4 - Phosphate; SO_4 - Sulphate; Alk - alkalinity; Si - Silicon; T_{min} - minimum temperature; T_{max} - maximum temperature; TBio - riffle instantaneous temperature; %OxBio - % riffle oxygen; Mg - Magnesium; and pH.

Table 8.21 Best-fit results for forward, stepwise multiple regression of the densities of flow indicator taxa from specific biotopes against physical habitat (including discharge) and water chemistry for each site. ^{H} - physical habitat; ^{C} - chemistry; ^{B} - both. Highly significant results ($P \leq 0.001$) are shaded.

SITE	EL				MO				DU				RI			
TAXON	**F (n, df)**	***P***	***R^2***	***var(s)***	**F (n, df)**	***P***	***R^2***	***var(s)***	**F (n, df)**	***P***	***R^2***	***var(s)***	**F (n, df)**	***P***	***R^2***	***var(s)***
Simuliidae - riffles																
	$^{B}(3, 8) = 22.457$	0.000	0.85	TotN, Fr, NBV	$^{C}(6, 5) = 30.206$	0.001	0.94	TBio, Na, Mg, Si, SO_4, Alk	$^{H}(1, 10) = 13.631$	0.004	0.58	VD_{ratio}	$^{B}(3, 8) = 6.411$	0.016	0.60	pH, %OxBio, v≤0.01%
***Notocladius capicola* - riffles**																
	$^{H}(4, 3) = 25.605$	0.012	0.93	d≤0.05%, $SUBd_{50}$, WW-Bio, TI	$^{C}(4, 3) = 20.481$	0.016	0.92	T_{min}, PO_4, Cl, Mg	$^{C}(3, 4) = 12.148$	0.018	0.83	SO_4, Ca, Mg	$^{B}(5, 2) = 83.128$	0.012	0.98	WW-Bio, Tr%Wet, PatTot, NO_2, K
***Ablabesmyia dusoleili* - pools**																
	limited data	-	-	-	$^{B}(3, 4) = 14.279$	0.013	0.85	K, PatTot, NO_3	$^{C}(1, 6) = 61.306$	0.000	0.91	SO_4	$^{H}(1, 6) = 11.174$	0.016	0.65	$SUBd_{50}$

Vars: Fr - Froude number; VD_{ratio} - velocity: depth ratio; NBV - near-bed velocity; TI - turbulence index; d≤0.05% - water depth ≤ 0.05 m; v≤0.01% - mean column velocity ≤ 0.01 m s^{-1}; WW-Bio - riffle transect wetted width ; PatTot - total patch surface area; Tr%Wet - transect total wetted width as %; $SUBd_{50}$ - substratum median particle size; Na - Sodium; Mg - Magnesium; Ca - Calcium; K - Potassium; Cl - Chloride; TotN - nitrate and nitrite combined; NO_3 - Nitrate; NO_2 - Nitrite; PO_4 - Phosphate; SO_4 - Sulphate; Alk - alkalinity; Si - Silicon; T_{min} - minimum temperature; TBio - riffle instantaneous temperature; %OxBio - % riffle oxygen; and pH.

8.7.1 Responses to low-flow disturbance history based on monthly flow indices

Identification of the best subset of flow indices for an analysis of invertebrate response to low-flow disturbance history was based on a combination of the group affinities of individual flow variables identified as potentially ecologically relevant (Figure 4.10) and simple linear regression of each variable against the densities of individual taxa (Table 8.22). There were no significant regression results for the monthly CV of flow against invertebrate taxa, but 15 of the other monthly flow indices examined were connected with faunal response (Table 8.22). A total of 73 significant relationships, nine of them highly significant, were found for 22 of the 32 most common taxa (Table 8.22). Of these relationships, more were negative, and sometimes consistently so for all families (e.g. monthly flow volume and monthly average discharge). The highest numbers of significant relationships with invertebrate families were found for Q_{inst} expressed as a flow percentile, Q_{min}, Q_{max}, median Q_{7dLow} and Q_{50}. The monthly low flow percentiles, Q_{75} to Q_{99}, did not correlate particularly strongly with individual taxon densities, with significant responses only for Acarina, Athericidae and Libellulidae. A number of taxa seemed to be favoured (in terms of population densities) by a seasonal low-flow disturbance regime characterized by lower magnitude values for monthly indices such as the Q_{min}, median Q_{7dLow} and Q_{50}, namely: Elmidae, Oligochaeta, Leptoceridae, Notonemouridae, and Hydroptilidae. In contrast, taxa including the Hydropsychidae, Baetidae, Acarina, Philopotamidae, Limnichidae, Leptophlebiidae, Pyraustidae, and in particular the Heptageniidae, appeared to respond positively in terms of mean densities to monthly indices that reflected naturally higher low flows over the dry season.

The results of a BIOENV assessment of the extent to which invertebrate assemblage composition in ordination space (stress = 0.15) could be explained by the most potentially ecologically relevant, monthly-level flow indices across the sites are presented in Table 8.23. The limited data set precluded site-specific analyses. The monthly flow indices found to be most influential in combination in structuring invertebrate assemblages, though weakly so, were Q_{max}, median Q_{7dlow} and Q_{95}. Instantaneous flows exerted less of an influence on assemblage composition than these measures, which reflected the high to low flow range experienced by the benthos in the long term. Other low flow percentiles assessed, particularly Q_{75} (and to a lesser extent, Q_{80} and Q_{90}) were quite similar in influence to Q_{95}, as anticipated given the high degrees of index inter-correlation.

Assemblage composition linked to monthly flow indices and reach abiotic conditions

When a series of physical habitat (hydraulics and habitat patch metrics) and chemical variables representing abiotic conditions at the time of flow disturbance were included alongside monthly flow indices, a vastly improved fit with assemblage composition was obtained (Table 8.23). Although a high number of variables (14) were required to optimize the match, similar results were obtained with five or even fewer variables. The most relevant flow indices included those of significance in the analysis of indices reflecting monthly

flow history (Q_{max}, Q_{95} or Q_{75}). Median Q_{7dLow} appeared less influential than a number of physical habitat and chemical variables, however, and instantaneous flow conditions assumed limited importance. Of the habitat variables found to be most relevant at low flows for invertebrates, based on the final results (Table 8.23) and BIOENV analyses for variable subsets, the majority represented the amount of wetted habitat available throughout the reach (WW, Tr%Wet, PatSATotWet, $SUBd_{50}$), its degree of connectivity (NoCh), and whether or not it provided flowing water conditions ($v \leq 0.01$ m s^{-1}, NBV or similarly, Fr) (Chapter 6). The chemical variables shown to have the most distinct bearing on assemblages at reach scale (Table 8.23, and BIOENV analyses for only chemistry) were the minimum monthly temperature, Mg^{2+} and $C\ell^{-}$ salts, alkalinity, total Nitrogen, PO_4-P, pH and EC.

Table 8.22 Significant results for simple linear regression of the densities of the 32 most common invertebrate taxa against monthly flow indices, based on pooled site data (*N* = 24). Pearson correlation coefficients and P values are presented in parentheses, with highly significant relationships in bold italics; (+/-) indicates the sign of the relationship. Taxon densities were fourth-root transformed. See Table 3.3 for flow variables and abbreviations. Flow percentiles were standardised by Q_{50}. ^{T} - log-transformed.

FLOW VARIABLE	TAXA
Volume^{T}	Athericidae (- 0.59, 0.002), Leptoceridae (- 0.59, 0.002), Acarina (- 0.56, 0.004), Notonemouridae (- 0.49, 0.014), Corydalidae (- 0.43, 0.034)
$Q_{inst}{}^{T}$	Leptoceridae (- 0.48, 0.019), Veliidae (- 0.40, 0.050)
Q_{inst} as flow percentile^{T}	***Heptageniidae (+ 0.72, 0.000)***, ***Hydropsychidae (+ 0.67, 0.000)***, ***Teloganodidae (+ 0.65, 0.001)***, ***Pyraustidae (+ 0.63, 0.001)***, Hydroptilidae (- 0.60, 0.002), Philopotamidae (+ 0.58, 0.003), Leptoceridae (- 0.56, 0.005), Notonemouridae (- 0.53, 0.007), Athericidae (- 0.52, 0.009), Elmidae (- 0.49, 0.014)
Monthly slogx^{T}	Athericidae (- 0.56, 0.005), Acarina (- 0.52, 0.009), Leptoceridae (- 0.46, 0.022), Veliidae (- 0.42, 0.040)
Monthly IV	Athericidae (- 0.49, 0.015), Libellulidae (+ 0.43, 0.037)
Monthly $Q_{mean}{}^{T}$	Acarina (- 0.57, 0.003), Athericidae (- 0.57, 0.003), Leptoceridae (- 0.56, 0.004), Notonemouridae (- 0.48, 0.017), Corydalidae (- 0.43, 0.035)
Monthly Q_{min}	Heptageniidae (+ 0.61, 0.002), Elmidae (- 0.56, 0.004), Oligochaeta (- 0.47, 0.021), Pyraustidae (+ 0.47, 0.021), Philopotamidae (+ 0.45, 0.027), Leptoceridae (- 0.43, 0.037), Hydropsychidae (+ 0.42, 0.043)
Monthly $Q_{max}{}^{T}$	***Notonemouridae (- 0.72, 0.000)***, ***Leptoceridae (- 0.67, 0.000)***, ***Athericidae (- 0.65, 0.001)***, Hydroptilidae (- 0.57, 0.004), Caenidae (- 0.56, 0.004), Empididae (- 0.50, 0.013), Acarina (- 0.48, 0.018), Tipulidae (- 0.47, 0.021), Heptageniidae (+ 0.46, 0.025)
Monthly median $Q_{7dLow}{}^{T}$	***Heptageniidae (+ 0.72, 0.000)***, ***Elmidae (- 0.64, 0.001)***, Baetidae (+ 0.61, 0.002), Hydropsychidae (+ 0.60, 0.002), Notonemouridae (- 0.55, 0.005), Philopotamidae (+ 0.55, 0.005), Leptoceridae (- 0.53, 0.007), Leptophlebiidae (+ 0.49, 0.014), Hydroptilidae (- 0.47, 0.020), Limnichidae (+ 0.41, 0.045)
Monthly $Q_{50}{}^{T}$	Leptoceridae (- 0.57, 0.004), Acarina (- 0.56, 0.005), Heptageniidae (+ 0.53, 0.008), Elmidae (- 0.52, 0.009), Notonemouridae (- 0.49, 0.015), Athericidae (- 0.46, 0.022)
Monthly $Q_{75}{}^{T}$	Acarina (+ 0.51, 0.011), Libellulidae (- 0.47, 0.021), Athericidae (+ 0.43, 0.035)
Monthly $Q_{80}{}^{T}$	Acarina (+ 0.49, 0.014), Libellulidae (- 0.48, 0.017), Athericidae (+ 0.44, 0.034)
Monthly $Q_{90}{}^{T}$	Acarina (+ 0.52, 0.009), Libellulidae (- 0.48, 0.018), Athericidae (+ 0.42, 0.042)
Monthly $Q_{95}{}^{T}$	Acarina (+ 0.57, 0.004), Libellulidae (- 0.43, 0.035)
Monthly $Q_{99}{}^{T}$	Acarina (+ 0.55, 0.005), Libellulidae (- 0.46, 0.024)

Table 8.23 Results of BIOENV analyses of combinations of monthly flow measures that independently, or in combination with variables representing reach habitat and chemical conditions, produced the best matches with a non-metric MDS ordination of invertebrate assemblages. Assemblage composition was based on monthly mean densities per taxon for the 32 most common taxa from site control locations. Best variable combinations are given for k ≤ 5 variables, and for the number of variables required for best overall match where k > 5. ^{T} - log-transformed. Flow indices standardised by Q_{50} where appropriate.

k	BEST VARIABLE COMBINATION(S) (ρ)	
	Flow variables	**Flow, habitat and chemical variables**
1	Q_{75}^{T} (0.21)	WW^{T} (0.54)
2	Q_{max}^{T}; Median Q_{7dlow}^{T} (0.30)	WW^{T}; $NoCh^{T}$ (0.59)
3	***Q_{max}^{T}; Median Q_{7dlow}^{T}; Q_{95}^{T}; (0.34)***	$NoCh^{T}$; T_{min} or Mg; $TotN^{T}$ or v≤0.01 (0.62)
4	Q_{max}^{T}; Median Q_{7dlow}^{T}; Q_{75}^{T}; Q_{95}^{T}; (0.32)	Q_{95}^{T} or Q_{75}^{T}; $NoCh^{T}$; $TotN^{T}$; v≤0.01 or $NoCh^{T}$; T_{min}; Mg; $TotN^{T}$ (0.65)
5	Q_{min}; Q_{max}^{T}; Median Q_{7dlow}^{T}; Q_{80}^{T} or Q_{75}^{T}; Q_{95}^{T}; (0.31)	$NoCh^{T}$; v≤0.01; Q_{95}^{T} or T_{min}; Mg; $TotN^{T}$ or Tr%Wet or WW, $NoCh^{T}$; v≤0.01; T_{min}; Mg or Q_{95}^{T}; $NoCh^{T}$; v≤0.01; pH; $TotN^{T}$ or Q_{75}^{T}; $NoCh^{T}$; v≤0.01; Mg; $TotN^{T}$ (0.66)
14	-	***Q%; Q_{max}^{T}; Q_{75}^{T}; $NoCh^{T}$; v≤0.01; NBV; $SUBd_{50}$; Tr%Wet; pH; T_{min}; Alk; Mg; PO_4^{T}; $TotN^{T}$ (0.70)***

Flow variables (Chapter 4): Q% - Q_{inst} as a percentile; Q_{min} - minimum monthly discharge over record; Q_{max} - maximum monthly discharge over record; median Q_{7dlow} - monthly median 7-day low flow over record; Q_{75} to Q_{95} - percentiles derived from monthly FDCs.
Chemical variables (Chapter 5): TotN - total Nitrogen; PO_4 - Phosphate; Alk - alkalinity; T_{min} - minimum monthly temperature; Mg - Magnesium; and pH.
Physical habitat variables (Chapter 6): NBV - near-bed velocity; v ≤ 0.01 m s^{-1} (equivalent to % flowing water) - mean proportion of channel transect with zero to non-flowing water; WW - channel wetted width (including standing water); NoCh - mean number of channels (i.e. flowing sections across the channel); Tr%Wet - mean transect total wetted width as %; $SUBd_{50}$ - overall substratum median particle size.

8.7.2 Responses to low-flow disturbance history based on annual flow indices

With the limitation of only four sites, it was not possible to conclusively demonstrate links between long-term annual measures of low flow and benthic invertebrate composition, based on mean densities at natural low flows. While some flow indices were clearly of greater influence on taxa than others, and a number of basic trends were evident, the results should be treated with caution. It is acknowledged that certain variables included in the annual suite effectively reflected conditions that spanned intermediate monthly to annual timeframes or were not calculable for each month (e.g. CV Dry, CV Feb, *P*-low).

A first assessment of the strength of relationships between annual flow variables and individual taxa highlighted a number of flow variables (21) that were of particular influence, with 41 significant

relationships across the 32 taxa examined, as indicated in Table 8.24. Though correlations were often very strong, they were based on so few observations as to be treated as only indicative of trends. Flow variables that, in contrast, did not bear much influence on the mean abundances of any invertebrate families were the absolute Q_{min} on record, and the corresponding CV (CV Q_{min}), as well as the median Q_{7dLow}, Q_{50} and Q_{80}. Several different taxa were linked to differences in annual, as compared with monthly, flow indices. Moreover, far more significant relationships were found among invertebrate families and monthly flow indices than annual indices, though across a similar total number of families (cf. Table 8.22). Twenty of the 32 most common taxa across the sites were responsive to annual measures of flow disturbance history (and with a near even balance between positive and negative trends), especially Caenidae, Hydraenidae and two odonate families (Table 8.24). A number of families, including the Teloganodidae, Hydraenidae and Corydalidae, showed positive relationships with indices reflecting higher degrees of flow predictability (and its components), both annually and during the peak of the dry season (e.g. *P*, *P*-low, *C*), and negative relationships with flow regime variability (e.g. CV, CV Dry, and similar measures) and indices reflecting high flow patterns (Table 8.24). Similarly, for example, caenids were positively associated with low flow percentiles, with higher densities at higher values of Q_{90}, Q_{95} and Q_{99}, but negatively linked with flood events (Q_5) and their year-to-year variability (IV).

Acknowledging the limited scope of a BIOENV analysis for matching overall natural assemblage composition at the sites with annual variables reflecting the longer-term flow history, some of which were over narrow ranges (e.g. *P*) the BIOENV results merited an overview. Excellent matches (correlations close to unity) were found on the basis of the following key variables in various combinations: Q_5, Q_{mean}, Q_{50}, Q_{95}, annual flow volume, and flow regime predictability (*P*) and constancy (*C*). The low-flow variables MAM, Q_{99}, Q_{90} and flow contingency (M) were also fairly influential. Flow variables found to be less useful in effectively separating site assemblages in ordination space were the annual CV, ARI 1:2 flood, Q_{max}, median Q_{7dLow} and Q_{80}.

8.8 DISCUSSION

Characterization of low flows that were ecologically meaningful for benthic macroinvertebrates was challenging, because trajectories or thresholds of response to flow disturbance were fewer, and typically less apparent or consistent, than those for physical habitat (Chapter 6). An approach modified from that traditionally used to identify influential flows based exclusively on habitat hydraulics (Section 8.1.2), however, revealed marked invertebrate responses in terms of immediate declines from natural in both the degrees of biotope specificity and tolerances for local hydraulics with artificial discharge reduction. Importantly, these changes in the nature of invertebrate relationships with altered quality of physical habitat were suggested by and intimately connected with the invertebrate redistributions observed across reach biotope mosaics, as habitat suitability and availability declined at low flows (Chapter 7). The inclusion of additional factors reflecting instantaneous discharge, physical habitat quantity, and subtler changes in water

quality (Chapter 5) at extremely low flows more fully described the immediate conditions influencing biological response. Exploration of the extent to which assemblage response in the short-term was intimately related to, and thus, could be characterized by longer-term windows of hydrological disturbance history based on flow indices (Chapter 4) contributed further understanding of how invertebrate response might be tied to patterns of flow variability, as well as to low and high flow events to which the benthos was naturally adapted.

Table 8.24 Significant results for simple linear regression of the densities of the 32 most common invertebrate taxa against annual flow indices for the sites (*N* = 4). Pearson correlation coefficients and P values are presented in parentheses. Taxon densities were fourth-root transformed. Flow variables are explained in Table 3.3, and were standardised by Q_{50} where appropriate.

FLOW VARIABLE	TAXA
Volume	Tipulidae (- 0.99, 0.013), Hydraenidae (- 0.96, 0.039), Simuliidae (- 0.96, 0.040), Ceratopogonidae (- 0.95, 0.048)
Volume Dry	Heptageniidae (- 0.98, 0.023), Baetidae (- 0.97, 0.028), Elmidae (+ 0.96, 0.043), Aeschnidae (- 0.96, 0.044)
P	Teloganodidae (+ 1.00, 0.000)
C	Teloganodidae (+ 0.98, 0.016)
M	Libellulidae (+ 0.99, 0.013)
P-Low	Aeschnidae (+ 0.98, 0.020), Leptophlebiidae (+ 0.95, 0.047)
C-Low	Hydraenidae (+ 0.99, 0.009), Simuliidae (+ 0.99, 0.011)
M-Low	Hydropsychidae (+ 0.99, 0.012)
CV	Libellulidae (- 0.99, 0.005), Chironomidae (- 0.99, 0.009)
CV Dry	Aeschnidae (- 0.99, 0.006)
CV Feb	Corydalidae (- 0.99, 0.009)
CV median Q_{7dLow}	Libellulidae (- 0.97, 0.030), Gyrinidae (- 0.96, 0.043)
IV	Caenidae (- 0.95, 0.047)
ARI 1:2	Pyraustidae (+ 0.99, 0.015)
Q_5	Caenidae (- 0.99, 0.008), Hydraenidae (- 0.98, 0.016), Simuliidae (- 0.96, 0.041)
Q_{mean}	Simuliidae (- 0.98, 0.019), Leptophlebiidae (- 0.97, 0.031), Hydraenidae (- 0.96, 0.040)
MAM	Corydalidae (+ 0.99, 0.007)
Q_{max}	Libellulidae (- 0.99, 0.008), Chironomidae (- 0.95, 0.050)
Q_{90}	Ceratopogonidae (+ 0.98, 0.018), Notonemouridae (+ 0.98, 0.024), Caenidae (+ 0.97, 0.028)
Q_{95}	Caenidae (+ 0.98, 0.018)
Q_{99}	Notonemouridae (+ 0.99, 0.014), Ceratopogonidae (+ 0.97, 0.027), Empididae (+ 0.96, 0.038), Caenidae (+ 0.95, 0.045)

8.8.1 Ecologically relevant low flows inferred from broad invertebrate-biotope associations

Invertebrate-biotope associations at naturally low flows

Under natural dry-season flows some 30 invertebrate families, representing 58% of all families common to the perennial rivers, exhibited distinct preferences for biotope type (Sections 8.3 and Section 7.8.2 provide details on specific taxa) from among hydraulically discrete riffles, runs and pools (see Chapter 6). Highly significant preferences among all hydraulic biotopes were only encountered for Simuliidae and

Hydropsychidae, both of which showed a marked preference for riffles, also by far the preferred biotope for a further six families. Though fewer, families preferring pools typically showed a high degree of specialisation for such environments (e.g. notonectids, naucorids, dytiscids and coenagrionids; Scholtz and Holm 1985; De Moor *et al.* 2003b). They also included the only families appearing uniquely associated with a particular biotope type at low flows, at least for the dominant biotopes investigated. Runs represented streambed patches of intermediate or marginal suitability for the majority of invertebrate families, except the Heptageniidae, underscoring their general role as low flow refugia (Sections 7.8.2 and 7.8.4). A lesser 22 families were biotope generalists, with no obvious preference for a particular hydraulic biotope or biotopes at natural dry season discharges. It is acknowledged that in instances where the same family showed the use of both riffle and pool environments (e.g. Leptophlebiidae), different flow-specialised species were probably responsible for the overall pattern of association. The intent here though was to mechanistically examine any observed changes in that pattern as an indication of a disturbance response, as the primary emphasis. Interestingly, at species level a lesser 17 or 38% of the 45 chironomid species recorded from across the study rivers also showed significant preferences for the habitats of particular biotopes at natural low flows, suggesting that this family might comprise a fair number of flow generalists. Other studies of low-flow disturbance have variously shown flow sensitivity or tolerance for this family (Fisher and LaVoy 1972; Ladle and Bass 1981; Cushman 1985; McElravy *et al.* 1989; Weisberg *et al.* 1990; Poff and Ward 1991; Castella *et al*. 1995; Growns and Growns 2001; Dewson *et al*. 2007a, b). Riffles remained the preferred biotope type for most species, with particularly strong specificity exhibited by *Notocladius capicola*, *Rheotanytarsus fuscus* and *Cricotopus* spp. Select species showed preferential utilisation of dry season pools, notably the tanypods, *Ablabesmyia dusoleili* and *Paramerina* spp.

That the invertebrate assemblages associated with different hydraulic biotopes at natural low flows, and hence particular complexes of microhabitat hydraulics comprised specific aggregations of taxa of differing relative abundances, underscored the powerful influence of the low flow regime through local habitat conditions. More importantly, it also confirmed the hydraulic biotope's ecological relevance as a mesohabitat patch unit, first demonstrated through an assessment of biotope assemblage composition and patch dynamics with flow regime in Chapter 7. Thus, the still largely open question of Wadeson (1996) and Padmore (1998, p. 33) as to "whether biota are sensitive to statistically significant, but subtle, differences in hydraulics and substrate size distributions which characterise visually identifiable biotopes" was answered. Grundy (1996, cited in Newson and Newson 2000) was one of few studies that similarly addressed this topic, for physical biotopes in the U.K.

From among other mesohabitat-scale studies (Section 8.1.1), the vast majority demonstrated similarly clear associations of the benthos with different mesohabitats for which some level of hydraulic distinctness was apparent under natural flow conditions (Logan and Brooker 1983; Gurtz and Wallace 1984; Pridmore and Roper 1985; Palmer *et al.* 1991; Boulton and Lake 1992a; Armitage *et al*. 1995; Wohl *et al.* 1995; Pardo and Armitage 1997; Beisal *et al.* 1998; Tharme and King 1998; Kay *et al*. 1999; Wood *et al*. 1999; Choy *et al.*

2000; Buffagni 2001; Brunke *et al.* 2001). Conversely, in fewer instances a gradient of association of invertebrate assemblages with mesohabitats was more evident that discrete relationships though taxa still showed some degree of hydraulic habitat preference, such as in U.S. Grant Creek (Sheldon and Haick 1981), as well as in habitats of the heterogeneous upper Acheron River, Australia (Barmuta 1989). Consistent with this study, Palmer *et al.* (1991) found strong evidence of association of macroinvertebrate species assemblages with eight visually defined, erosional and depositional biotopes defined primarily on hydraulic grounds, in the Buffalo River, Eastern Cape, South Africa. Of 27 common taxa examined, 13 showed biotope specialisation in that they occurred in a single biotope in more than 50% of the samples in which they were collected. As in the present study, most species were distributed across several biotopes, but with the most distinct species-biotope association for riffles; there were no unique taxon-biotope associations in the Buffalo R.. Hydropsychidae and mayflies were riffle indicators occurring more than 85% of the time, two groups also strongly linked to riffles here. Palmer *et al.* (1991) noted that biotope-level patterns masked subtleties in species distributions that extended beyond those biotopes defined. Speculatively, their finding reflects an underlying influence of microflow regimes (though other factors might equally have been responsible), as shown at low flows in the current study (Sections 7.5 and 7.8). In a comparison of macroinvertebrate assemblages from biotopes in three N.Z. streams, while the majority of taxa (63-68%) were similarly abundant in riffles and runs, some were more abundant in the former habitat and only at most 12% in runs (Pridmore and Roper 1985). Yet, no more than two taxa in any one stream were exclusive to riffles. Even across 17 diverse studies of principally upland rivers of the U.K. and North America, riffles and pools had similar numbers of taxa, and from the same suite of families and species groups (Logan and Brooker 1983). Of more than 70 families, only six were riffle restricted, including Helodidae and Blepharoceridae, and fewer were pool dependent (e.g. Coenagrionidae, Corixidae and Gyrinidae), but with considerable variation encountered across rivers. Only the Baetidae and Simuliidae showed significant differences in density between riffles and pools, always with greater densities in the former habitat (as in this thesis) and with several *Simulium* species restricted to riffles.

Shifts in biotope specificity with extreme low flows

Against the established baseline of natural hydraulic biotope-invertebrate associations, artificial discharge reductions to extremes had a singularly obvious threshold effect. A dramatic loss in biotope specificity occurred with at least 20 families no longer showing detectable among-biotope preferences, encompassing fully two-thirds of those families exhibiting significant specificity at natural low flows. Furthermore, the strengths of association with different biotopes for those taxa that still showed some specificity had also detectably declined. The same trend was apparent for five chironomid species, representing 29% of those species with previously significant biotope associations. In the majority of instances, the shifts reflected an intensified association of rheophilic taxa with slower-flowing biotopes, though simuliids and *Notocladius capicola* retained the strongest biotope associations of all families and chironomid species, respectively.

While other studies have not addressed this aspect of low-flow disturbance in this way, there is at least some evidence to support shifts in the nature of assemblage-biotope associations at very low flows. A breakdown occurred in the pattern of physical discontinuities between various biologically discrete mesohabitats at extreme low flows in perennial Mill Stream, England, that resulted in minimal detectable differences in invertebrate richness and species composition among certain of the mesohabitats (Pardo and Armitage 1997; Chapter 6). As in the present study (Chapter 7), some invertebrates simply extended their distributions from marginal to more mid-channel areas in response to the disturbance. While more flow-permanent sites on the intermittent Lerderderg River, Australia, consistently exhibited biotope-specificity of their assemblages, invertebrate composition between riffles and pools overlapped considerably in a more temporary site on the intermittent Weerribee River (Boulton and Lake 1992a). The distinction among sites was perhaps evidence of diminishment of the strength in biotope-invertebrate associations along a flow permanence gradient, as observed in the current study within a single river flow type under different degrees of discharge reduction.

It is recognised that certain changes in biotope associations at summer low flows might also reflect behavioural or other factors for particular taxa. Presumably then, however, they would have also been reflected in the natural patterns of biotope association described above, and would not have been consistent for multiple families and species. Higher *Rheotanytarsus* densities in a pool at one site on the upper Wye River, where larvae were predominantly early instars, as compared with other locations where there were no differences in densities between pools and riffles when only later instars were present, suggested the difference might be due to adult oviposition behaviour rather than biotope association (Wisniewski 1978, cited in Logan and Brooker 1983). In another example, Boon (1979, cited in Logan and Brooker 1983) indicated that older *Hydropsyche* larvae initiated natural biotope shifts prior to emergence, migrating from riffles to pools.

Clearly, biotope-family associations were an extremely useful, as yet underexplored (Section 8.1.1) coarse-scale measure of potential thresholds of biotic response to low-flow disturbance. Further, they proved a valuable screening tool for identifying families with the greatest potential as flow indicators, through their mesohabitat preferences and how those transformed with artificial flow reduction. As discussed in the next section, the loss of detectable biotope specificity for many taxa was corroborated by evidence of losses in the strengths of invertebrate relationships with one or typically more hydraulic factors, collectively and for individual taxa, with flow reduction below normal levels.

8.8.2 Low-flow disturbance in the context of invertebrate hydraulic tolerances

A quite different suite of hydraulic indices assumed significance in influencing the responses of invertebrate assemblages to low-flow disturbance than typical at high flows, as water levels were lowered and bed elements exposed to strong alterations in local hydraulics. Shear velocity and stress, for instance, appeared less influential in structuring invertebrate assemblages at very low flows than reported with flood disturbances (Statzner 1981a; Gordon *et al*. 1992; Death and Winterbourn 1995; Jorde 1996; Matthaei *et al.*

1997, 2000; Jorde and Bratrich 1998; Imbert and Perry 2000; Jowett 2003), while variables such as VD_{ratio} assumed greater influence at lower flows. Certain hydraulic factors retained their biological importance despite the abnormal reductions in discharge, notably Froude number and near-bed and mean column velocities, confirming them as among the more universal hydraulic indices for ecohydrological work and appropriate for studies of low-flow disturbance (Jowett 1993; Wadeson 1996; Padmore 1997; Wadeson and Rowntree 1998; Vadas and Orth 1998; see also Chapter 6 and Section 8.1.2).

Invertebrate relationships with hydraulic factors at natural low flows

That the benthos was effectively 'integrating' local hydraulic conditions (Statzner *et al.* 1988) under natural dry season conditions was irrefutable. There were many instances of significant or highly significant relationships among 38 invertebrate families and 26 chironomid species, and one or more of the ten principal hydraulic indices that effectively physically characterized biotopes (Chapter 6). Thus, both standard and composite hydraulic indices were able to adequately represent the low flow-relationships of various invertebrate taxa in the present study, as asserted by Gore (1998) and Jowett (2003). Though seldom connected with the hydraulic characterization of mesohabitats at the same time (but see, for example, Brunke *et al.* 2001) or focused specifically on aspects of low-flow disturbance, similarly well developed relations between invertebrate taxa and hydraulic indices have been widely demonstrated (as reviewed in Gore 1987, 1989; Statzner *et al.* 1988; Campbell 1991; Jowett 2003; specific references are provided in Section 8.1.2).

In the present case, consistent generic relationships with various hydraulic variables, many of which were of course intercorrelated (Statzner *et al.* 1988; Gordon *et al*. 1992; Quinn and Hickey 1994; Jowett 1993, 2003), were apparent across rivers for common invertebrate taxa at natural low flows. Such relationships were often stronger, and arguably more representative (Bovee 1986; Tharme 1996; Gore and Nestler 1988), however, when considered independently by river. Generalised relationships have also been generated for invertebrate taxa across multiple streams in the U.S.A. (Gore *et al.* 2001) and New Zealand (Jowett and Richardson 1990; Jowett *et al*. 1991; Jowett 2003) with varying degrees of success. Correlations between *Deleatidium* abundances and a joint suitability function calculated from generalised velocity, depth and substratum curves were weak but significant, in four N.Z. rivers (Jowett and Richardson 1990; Jowett *et al*. 1991). However, a habitat suitability curve for Fr created for all rivers combined predicted *Deleatidium* abundances in two of the rivers better than any river-specific or generalised curves based on velocity, depth or substratum.

Significantly stronger associations with several hydraulic variables than in general were observed for certain families in the present study for particular rivers, as was the case for notonemourid stoneflies in the mountain-stream reach of the Riviersonderend River. The latter result suggested that this recognised flow-hydraulics sensitive group (Ward and Stanford 1979; Williams and Winget 1979; Growns and Growns 2001) responsive to both short- and long-term flow disturbance histories (Saltveit *et al*. 1987), might have singular potential as a flow indicator for this river. Such distinctions in invertebrate-hydraulics relationships accorded

with the fact that although biotopes maintained their hydraulic integrity across rivers, there were differences in the degree to which individual types did so, as well as in the hydraulic variables most responsible for inter-biotope differences in the individual rivers (as described in Chapter 6). Correspondingly, the hydraulic variables most influencing invertebrate assemblage patterns varied in different rivers, but with some consistency in those most biologically influential. The same was true for relationships between *Deleatidium* abundances and hydraulic factors across the N.Z. rivers studied by Jowett *et al*. (1991).

Families and species possessed different degrees of responsiveness to local hydraulics and dependencies on particular hydraulic variables from within the array that combined to reflect local conditions at natural low flows. As to be expected, given the range of biotope and microhabitat preferences invertebrates exhibited, while certain hydraulic factors were typically more influential than others, they were not necessarily the same ones across different taxa (Statzner *et al*. 1988; Campbell 1991; Jowett *et al*. 1991; Aadland 1993; Quinn and Hickey 1994; Gore 1998; Jowett 2003; Section 8.1.2). A core group of some 17 invertebrate taxa, the majority dominant in riffle environments, were highly responsive to almost all hydraulic factors examined. All of the families and species that exhibited high biotope specificity at naturally low flows (Section 8.3) were unsurprisingly among this group, showing highly significant and in many instances fairly strong relationships with hydraulics. As a previously demonstrated riffle indicator (Section 7.4) the Hydropsychidae, exclusively comprising two *Cheumatopsyche* spp. dependent on hydraulics for their net-based mode of feeding (Edington 1965, 1968; Alstad 1982; Scott 1983), were particularly strongly influenced by local hydraulics. They were the sole family significantly positively correlated with all hydraulic indices, except directly with water depth (cf. the effect of manipulated low flows below). Similarly, only one chironomid species of those examined, *Rheotanytarsus fuscus*, showed highly significant positive correlations with all hydraulic indices except depth (with which the relationship was negative, as it was for hydropsychids), supporting its established preference for riffles. *Rheotanytarsus* was similarly identified as a naturally flow sensitive genus by Weisberg *et al.* (1990) and Robson *et al*. (1999). The densities of substantively a further nine families or taxon groups and six other chironomid spp. were also firmly associated with most of the hydraulic factors typifying biotopes at natural summer discharges.

Many invertebrate families and chironomid species showed strong, predominantly positive relationships in abundances at natural low flows with a key suite of velocity-related habitat measures, from mean column and near-bed velocity (NBV), to Fr and VD_{ratio}, supporting well established general influences of current on the benthos (Ambühl 1959, cited in Hildrew and Giller 1994; Ulfstrand 1967; Chutter 1969; Ciborowski 1983; Brusven 1984; Statzner *et al*. 1988; Wetmore *et al*. 1990; Jowett *et al*. 1991; Campbell 1991; Armitage 1995; Uys and O'Keeffe 1997a; Jowett 2003; Lancaster and Belyea 2006). Given their distinct preference for riffles (Section 8.3) and velocity requirements for filter feeding (Chance and Craig 1986; Day *et al.* 2003), it was not unexpected that simuliids demonstrated the strongest association of all families with all these velocity-based variables. The strongest relationships with hydraulics of all Chironomidae species, including those primarily reflecting velocity, were apparent for *Notocladius capicola*, the species that showed the most

pronounced biotope (riffle) specificity. Although Froude number describes gross flow characteristics of the water column and at the surface, in terms of turbulence, rather than near-bed conditions (Newbury 1984; Statzner *et al*. 1988; Davis and Barmuta 1989; Gordon *et al*. 1992; Wadeson and Rowntree 1998), it too has correlated strongly with the distributions and abundances of different invertebrates across a diverse range of flow conditions (Gore 1978; Statzner 1981a, b; Orth and Maughan 1983; Wetmore *et al.* 1990; Jowett *et al.* 1991; Davis and Growns 1991; Jowett 1993; Quinn and Hickey 1994; Emery 1994; Gore 1996; King and Schael 2001). Although Fr has been more commonly used in biological studies, it has been anticipated that VD_{ratio} would be similarly effective as a descriptor of benthic habitat (Jowett 1993). The results of this study appear to be among the first in confirming this view, in that VD_{ratio} was not only highly influential in defining the hydraulic characteristics of biotopes at low flows (Section 6.4; see also Jowett 1993; Wadeson 1996; Wadeson and Rowntree 1998; Vadas and Orth 1998), but additionally their biological composition.

Although not specifically focused on low flows, significant relationships with 0.6V and Fr were revealed by microhabitat utilisation curves, for densities of all eight common ephemeropteran species of one of the rivers studied in this thesis, the Molenaars River, southwestern Cape (Paxton 2000). Additionally, strong variations in benthic invertebrate abundances with mean velocity were common across 673 locations representing a range of river flow regimes and hydraulic habitats, as were marked differences in the velocity preferences among species (Jowett 2003). Clear differences in the tolerance ranges and breadth of optima of four invertebrate species for velocity were also found in the River Spree, Germany (Brunke *et al.* 2001). Three of seven groups of New Zealand invertebrates showed specific velocity tolerances in the Waingawa River (Jowett and Richardson 1990). Moreover, several invertebrate taxa across local streams of differing size and flow regime similarly showed distinct preference ranges for velocity, with nine of 12 common taxa preferring high average velocities, as well as for Fr (Jowett *et al*. 1991; Quinn and Hickey 1994). In Glover Creek, U.S.A., although individually all hydraulic factors tended to exert relatively weak influences on the benthos, velocity was the most common hydraulic index of influence for riffle taxa (Orth and Maughan 1983). Froude number was third-most influential, with *Simulium*, *Cheumatopsyche* and *Chimarra* all exhibiting positive trends.

Naturally strongly positively associations with complex hydraulic variables in addition to Fr above, namely another index of turbulence (TI, previously unexplored at low flows; Padmore 1997), Reynolds number and roughness Reynolds number were shown by many families in the present study as well, including Simuliidae, Hydropsychidae, Chironomidae and Baetidae. Typically independently, these variables have been shown to be strong predictors of mesohabitat types (Wadeson 1996; Wadeson and Rowntree 1998; Vadas and Orth 1998) or of taxon densities. In the latter instance, for example, Reynolds number was the most useful predictor of densities of the water bug, *Aphelocheirus aestivalis*, followed by mean current velocity, viscous sublayer thickness, boundary Reynolds number, and then Fr (Statzner *et al*. 1988). In contrast, although a relationship was found between *Deleatidium* abundance and Reynolds number for four N.Z. rivers, Fr was more influential (Jowett *et al*. 1991). Density of the mayfly, *Rhithrogena*, was positively

correlated with turbulence intensity at different discharges in the Canadian Fraser River (Rempel *et al.* 2000).

The weakest associations of invertebrate families and species with microhabitat hydraulics at natural low flows were with depth, relative roughness (and its inverse, relative exposure), and substratum size. Although depth, in particular, was one of the most influential variables in biotope characterization on physical grounds (Section 6.4), the benthos responded rather to integrated representations of depth with other variables at natural low flows, though still relatively weakly in many instances. Depth has been shown to be one of the less influential hydraulic parameters for invertebrates, although not consistently so, among ecohydrological studies (Orth and Maughan 1983; Brusven 1984; Statzner *et al*. 1988; Jowett and Richardson 1990; Jowett *et al*. 1991; Armitage 1995; Clarke and Scruton 1997; Paxton 2000; Rempel *et al.* 2000; Jowett 2003). It was the least useful predictor, along with substratum character, of several hydraulic indices in representing the preferred habitat of *Aphelocheirus aestivalis* (Statzner *et al*. 1988). Although preferred depth ranges were apparent for the majority of common taxa across multiple N.Z. rivers, with most taxa preferring shallower waters, relationships between taxon relative abundances and depth were often weak and inconsistent (Jowett and Richardson 1990; Jowett *et al*. 1991; Jowett 2003); only the net-spinning trichopteran, *Aoteapsyche* spp., showed a distinct relationship. Only one common mayfly, *Lestagella* sp., showed a significant correlation between density and water depth in the Molenaars River, South Africa (Paxton 2000). Conversely however, in Glover Creek, U.S.A., depth was second only to velocity as an influential hydraulic factor for different invertebrate species, as well as for invertebrate diversity (Orth and Maughan 1983). The filter feeder, *Hydropsyche morosa* gp., showed highly specific depth requirements and was positively correlated with Re and substratum roughness across various discharges in the Fraser R. (Rempel *et al.* 2000).

In the current study, negative relationships with hydraulic factors although rare, were usefully indicative of those taxonomic groups with distinct natural preferences for pools and other slow-flowing environments. Such taxa included Corixidae, Notonectidae and Leptoceridae, all of which showed correlations with a substantial seven out of ten major hydraulic indices. Additionally, the abundances of two tanypods and an orthoclad were highly significantly, but negatively correlated with most variables, linked to naturally denser populations in pools at low flows. Comparatively fewer negative than positive relationships among taxa and hydraulic variables also appears predominant in other invertebrate-hydraulics studies. Of common mayflies in the Fraser River, *Heptagenia* and *Baetis* were negatively correlated with mean velocity and v_*, respectively (Rempel *et al.* 2000). For N.Z. streams, while strong positive relationships with velocity were apparent for *Aoteapsyche* spp. and the filter-feeding mayfly, *Coloburiscus humeralis*, a converse relationship was reported for a swimming mayfly, *Nesameletus* sp., as well as for naidids (Jowett *et al*. 1991; Quinn and Hickey 1994).

Decoupling of invertebrate-hydraulics relationships with artificial low-flow disturbance

With severe low flows induced artificially across multiple reaches a clear disturbance threshold was exceeded, in that the majority of invertebrates, whether families or species, lost all or most of their significant associations with habitat hydraulics. This strongly pointed to a decoupling of biotic response from the direct influence of hydraulic conditions described above. It also suggested that invertebrate distributions under severely reduced flows might be more immediately a function of the availability of still-wetted habitat than of its hydraulic quality, with invertebrates not inhabiting their expected, preferred instream habitats (Hart *et al*. 1996; Lancaster and Belyea 2006). Hydraulic variables for which the loss of a link with individual taxon abundances was most obvious were VD_{ratio}, Fr and roughness Reynolds number, closely followed by all other variables with which invertebrates had been strongly associated under pre-disturbance flows. Although there are as yet few, if any, studies with which to directly compare these results, the specific forms of established relationships shown by taxa for hydraulic factors (e.g. based on HSI curves; Section 8.1.2) are likely indicative of the weakening of links to those factors, as discharge magnitude alters.

None of the originally significant hydraulic relationships remained so for the Empididae, Athericidae, Hydroptilidae or Oligochaeta. Additionally, of those chironomid species with the highest number of significant correlations with microhabitat hydraulics at natural flows, almost all of them no longer showed any highly significant relationships, including the filter-feeding rheophile, *Rheotanytarsus fuscus*, naturally strongly attuned to patch hydraulics. Furthermore, all the taxa characteristic of pool environments that exhibited multiple highly significant, negative hydraulics-density relationships at natural low flows showed a decoupling of all such associations when flows were severely reduced. Those pool-dwellers most affected were the Leptoceridae, Corixidae and Notonectidae, as well as the chironomids, *Corynoneura* spp., *Ablabesmyia dusoleili* and *Paramerina* spp. The responses of such pool benthos reflected the marked physical changes observed in pool conditions and varied redistribution paths evident for pool fauna at extremely low flows (Section 7.8). For some pool taxa, as exemplified by *Ablabesmyia dusoleili*, while overall patterns of hydraulic habitat use were similar at both natural and extreme low flows, under the latter conditions their preference for standing waters diminished, suggesting certain pools were becoming limiting even for pool-adapted species. Supporting evidence was provided by trends in abiotic parameters observed particularly for shallow isolated pools in the highly flow altered reaches (Chapter 5, and Sections 6.5 and 6.7).

Only two families, Simuliidae and Chironomidae, and three species of the latter family (*Notocladius capicola*, *Cricotopus* spp. and *Rheocricotopus capensis*), within the fairly large group of taxa that showed numerous significant, positive density-hydraulics relationships at natural low flows, retained all of their strong links once flows were artificially reduced. For these and a few other taxa naturally most common in riffle patches, for indices with which highly significant relationships with abundances remained at reduced flows, the strengths of those hydraulic relationships intensified as habitat areas with such conditions declined

in availability. This consistent flow disturbance reaction across diverse hydraulic variables and taxonomic groups suggested there was a group of 'sensitive rheophiles' (*sensu* O'Keeffe *et al*. 2002) amidst the wider suite of riffle-preferring invertebrates, that exerted more precise microhabitat selection. Such hydraulic fidelity is well established for simuliids, with their need to maximise feeding efficiency and space partitioning among individuals (Chance and Craig 1986; Fonseca and Hart 1996; Hart *et al.* 1996; Statzner *et al*. 1997), among other obligate rheophiles (Ward 1976; Jowett *et al*. 1991; Campbell 1991, 1992; O'Keeffe and Dickens 2000); simuliids ceased filter-feeding entirely in highly flow-disturbed patches (pers. obs.). While Hydropsychidae were still most abundant in riffles and significantly positive correlated with measures such as NBV and Fr that reflected their hydraulic specialisation (Edington 1965, 1968; Alstad 1982), they showed a marked decrease in the overall number of such hydraulic relationships from that observed under natural low flows and limited intensified association with hydraulics. This suggested that the filter-feeding *Cheumatopsyche* were experiencing low-flow stress in their existing patches and/or had preferentially relocated to other microhabitats. The intolerance of this group to extreme low flows and pool-like hydraulic conditions following flow cessation, and consistent responsiveness to flow alteration, are well established (Larimore *et al*. 1959; Edington 1965; Hauer *et al*. 1989; McIntosh *et al*. 2002). When discharge and hence velocity patterns were experimentally altered in a U.K. stream, *Hydropsyche instabilis* not only ceased construction of food collection nets, but also declined in abundance in areas of low velocity, relocating to areas of preferred flow conditions (Edington 1965). Although with flow reduction of more than 92%, *Cheumatopsyche pettiti* densities responded positively to Froude number in a Hawaiian stream subjected to diversion (McIntosh *et al*. 2002), the extent to which the nature of the relationship may have changed from that at natural low flows was not established.

In a few instances, solely apparent for chironomid species, relationships between densities and biotope specificities or individual hydraulic factors became significant only under unnaturally low flows. Though difficult to demonstrate conclusively, as previously postulated (Section 7.8.2) these species might have been favoured by the altered hydraulic conditions and able to proliferate rapidly locally, due to their particular life cycle attributes. Alternatively, they might simply have been able to more effectively exploit resources under habitat conditions less favourable for other typical patch inhabitants (Extence 1981). For example, *Nanocladius* emerged with hydraulic specificity enhanced above natural levels for pools, appearing sufficiently favoured by the increased availability of slow-flowing environments under disturbance to increase in local densities.

Principal responses of invertebrates based on flow-mediated hydraulic tolerances

Based on the above shifts in hydraulic parameters elicited with experimental low-flow disturbance, two basic forms of biological response prevailed as patch conditions deteriorated, with the mix of hydraulic effects in any patch combined with the tolerance ranges of a particular taxon for those various changes instrumental in the outcome. It proved too difficult, as also reflected by Beisal *et al.* (1998), and appeared of little utility anyway, to discriminate among the individual effects of hydraulic variables on the invertebrate structure of

stream patches. In the majority of cases, invertebrate taxa appeared either to possess significant breadth of hydraulic tolerance or to be able to adapt in the short-term, so as to endure hydraulically marginal conditions as the availability of certain biotope types decreased and individual patch quality declined in the landscape. They either remained in the same patch, often passively and under crowded conditions, or were obliged to relocate to other wetted patches, redistributing using the pathways described in Section 7.8. Few taxa appeared to be living in their preferred microhabitats under very low flows. This was verified for multiple biotope indicator taxa for which shifts in habitat suitability with flow disturbance, examined using HSI curves, revealed that they possessed restricted scope to express true preference, due to the limited amount of suitable hydraulic habitat available at artificially reduced flows; complementary information was gained from these curves at family and species levels. Most invertebrates were presumably experiencing varying levels of flow-mediated hydraulic and related stress as a result (as suggested earlier for hydropsychids). Especially given the naturally narrower tolerances of certain taxa, typically associated with physiological or behavioural factors, such stress levels were improbably sustainable in the longer term at the same flow disturbance intensities. Less commonly, certain taxa demonstrated either an intensified effort by individuals to actively remain and fully exploit, or concentrate in, areas of optimal hydraulic conditions (see also Lancaster and Hildrew 1993a), where still feasible based on local patch and broader reach conditions, again reinforcing select redistribution paths observed at experimentally reduced discharges (Section 7.8). Even when the range of conditions utilised by such taxa was wider than that under natural low flows, actual preferences typically remained narrow. Families for which this pattern held true included the Elmidae, Chironomidae, Simuliidae and Baetidae. Also evident was that many such typically rheophilic taxa were constrained by their hydraulic tolerances and unable to make effective use of non- or barely flowing areas even in the immediate term.

Therefore, habitation by invertebrates of particular biotope patches at artificially reduced flows did not necessarily mean they were tolerant of what were clearly marginal hydraulic conditions. Further, the altered biotope specificity of some taxa at abnormal discharges might plausibly have been related to factors additional to hydraulics, such as otherwise deteriorating environmental conditions or, less well documented, enhanced biotic interactions among species (Peckarsky 1983; McAuliffe 1983, 1984). Regardless of such instances when biophysical factors have forced biota to reside in sub-optimal riverbed areas, often when characterizing the low flow needs of invertebrates instream habitat has been designated as 'available', 'usable' or even 'optimal' on the basis of occupancy alone (Bovee 1982). King and Tharme (1994, p. 278, Figure 9.22) first illustrated the importance of evaluating changes in the actual 'habitat value' of biotope patches with changing discharge, with specific reference to methods commonly adopted for calculating habitat suitability (e.g. weighted usable area, WUA, in PHABSIM; Stalnaker *et al*. 1994). Power *et al*. (1988) reinforced this point, arguing that evaluations of habitat quality needed to be supported by experimental and process-oriented studies. In the way in which they were used here, suitability curves proved particularly illuminating when contrasting the situation at natural and experimental low flows,

revealing shifts in invertebrate hydraulic preferences within overall tolerance ranges in response to different degrees of disturbance.

Invertebrate flow sensitivity and its utility

That it was possible to identify families and species with natural highly significant relationships with particular biotopes and associated hydraulics (even more so than based on direct relationships with discharge magnitude - discussed below) helped distil out the likely flow sensitive taxa. Presumably also, the numerous families and species shown to be natural biotope and hydraulics generalists could be expected to be less stressed with obligatory redistribution into less suitable patches with severe flow reduction than their more biotope-specific counterparts. Given the reality, however, that a significant complement of the benthos exhibited a highly developed ability, behavioural or otherwise, to adapt to or persist under marginal conditions, it might be simplistic to consider particular invertebrates as flow-hydraulics specialists at artificially low flows based simply on their relative occurrence in particular biotopes or microhabitats. The disturbance-driven breakdown of habitat preferences observed for most taxa in this study thus introduced a new dimension to the selection and use of flow indicator groups for ecohydrological research. It also raised the question as to what extent invertebrates had actually exceeded their hydraulic tolerances in the flow-disturbed patches they inhabited, and for how long they might withstand conditions in such temporary flow refuges. Invertebrate responses at unnaturally reduced discharges revealed that many taxa were largely outside their normal tolerance ranges.

Certain taxa were consistent indicators of biotope type and flow hydraulics at natural low flows and thus potentially useful sensors of declining flows and in different ways. As from other studies of invertebrate relations with hydraulics, the most suitable flow specialists seemed to be sensitive rheophiles with narrow hydraulic requirements (Ulfstrand 1967; Ward 1976; Statzner *et al*. 1988; Jowett *et al*. 1991; Campbell 1991, 1992; Fonseca and Hart 1996; O'Keeffe and Dickens 2000; Jowett 2003). Although less attention has been focused on pool taxa, the intolerance of several of them for high velocity environments made them potentially useful indicators of flow disturbance as well, at the other end of the biotope-hydraulics gradient. Separation into categories of flow sensitivity or tolerance has tended to be intuitive in the past (based on collective knowledge of taxon habitat associations or autecology) or based primarily on select indices reflecting direct hydraulic preference under natural flows (e.g. Extence *et al*. 1999; Growns and Growns 2001). Many invertebrates were shown to be highly flow adaptive here and it was possible, and indeed invaluable, to contrast taxon responses to artificial flow disturbance with their tolerances at natural low flows, and in terms of multiple hydraulic factors. Generally, such rigorous comparisons seem conspicuously scarce, constraining the depth of understanding of actual tolerance to flow stress (O'Keeffe *et al.* 2002; Chapter 9). In one interesting example, though based on a single hydraulic factor, a preference curve for the net-spinning *Hydropsyche instabilis*, of catch-net density as a function of unaltered near-bottom velocity, was successfully used to predict its responsiveness to velocity changes with experimental discharge alteration in Perlbach Stream, Germany (Statzner *et al*. 1990). *H. instabilis* larvae vacated streambed patches

intensely affected by NBV decreases with flow reduction. Similarly, relationships between an index of near-bed hydraulics based on FST-hemispheres (Statzner and Müller 1989) and discharge in the same stream, along with preference curves developed for representative species for similar streams elsewhere, were used to predict invertebrate population decreases with discharge reductions (Statzner *et al*. 1990). As a result of differences in their tolerances for altered near-bed hydraulics, while large population losses were modelled as likely with a certain magnitude discharge reduction for the stonefly, *Dinocras cephalotes*, the amphipod, *Gammarus fossarum*, was predicted to be less affected. Using established species preferences for bottom shear stress, it was possible to simulate with CASIMIR how deterioration of hydraulic habitat with discharge diversion favoured a limnophilous leech over rheophilic trichopterans, in the German Kocher River (Jorde and Bratrich 1998). In another case, differences in habitat suitability as a percentage of optimum versus average monthly discharge could be evaluated between pre-drought and extreme low-flow periods, based on the natural hydraulic tolerances of both *Sericostoma personatum* and *Limnius volkmari*, in a PHABSIM study of the River Babingley, U.K. (Petts *et al*. 1999).

Family-level response appeared adequate for purposes such as the development of flow sensitivity indices based on hydraulic factors, for routine river monitoring or flow management (Chapter 9) - though this remains a point of debate (Orth and Maughan 1983; Monk *et al*. 2007). As previously acknowledged in this thesis, and in part addressed through assessments at family and species level, the use of family-level data was potentially less precise in instances where different taxa within a family are known to possess variable requirements for hydraulic or hydrologic attributes (Extence *et al*. 1999; Monk *et al*. 2007). Though similar degrees and patterns of biotope specificities were evident for families and species, species-level analysis has the added potential of delineating groups of species with particular flow-related life history traits. This advantage might render species more useful in the detection of longer-term responses to flow disturbance history, for example when relating invertebrate response directly to annual flow indices (Section 8.8.4 and Chapter 9). Nevertheless, demonstrable benefits were gained here in increased understanding of response to flow alteration by using multiple invertebrate indicators and at varying levels of taxonomic resolution, with different taxa showing varied responses to the same unit of low-flow disturbance. Different invertebrates were also found to be more useful flow indicators in each river, though with a few families showing generic flow response patterns.

Comparison of the patterns of association of invertebrate taxa with biotopes, and the most influential hydraulic factors defining them under natural and extreme low flows, proved an extremely useful starting point for characterizing invertebrate response to low-flow disturbance. Where partial or complete loss of specificity occurred across multiple taxa of differing flow-hydraulics sensitivities, it represented a meaningful way of identifying thresholds of potentially significant disturbance-induced change (Chapter 9). Moreover, patterns of change in the degree of biotope and microhabitat specificity were effective in confirming common pathways of invertebrate response to flow reduction within the riverscape, and across multiple families. In characterizing ecologically meaningful low flows for invertebrates, full use has yet to

be made of such generalised responses of mesohabitat-invertebrate associations, flow-hydraulic habitat guilds, or even hydraulic tolerances of individual taxa, with proportional changes in the availability and hydraulic character of patch types with altered flow patterns. Moreover, as previously alluded to (Section 1.4.8), there remains a lack of scaling up of the knowledge gained from studies of microhabitat hydraulics to the mesoscale within the reach, while this is essential for improved understanding of the implications of disturbance and thus, effective river flow management (Armitage and Pardo 1995; Newson and Newson 2000; Whittington 2000).

8.8.3 Instantaneous discharge as a single index of low-flow disturbance

Direct family responses to discharge

The majority of invertebrate families responded to low-flow disturbance weakly and inconsistently when it was represented purely in terms of a single index describing immediate flows. Instantaneous discharge did, however, affect trends in the mean densities of 19 families across multiple rivers and hydraulic biotopes (species were not assessed). Fairly strong responses to discharge magnitude at the actual time of disturbance were only found for Notonemouridae (negative) and Acarina (positive), and were biotope specific. Furthermore, generalised relationships were possible for only two taxa, Leptoceridae and oligochaetes, both with declines in abundances with decreases in Q_{inst}. Many of the taxa established as biotope and hydraulics indicators showed significant direct relationships with the low flow index, but unsurprising not so those families for which densities totally decoupled from hydraulics at artificially reduced flows. Though plainly low flow-responsive, several taxa, including Baetidae, Chironomidae, Caenidae, Teloganodidae and Acarina particularly lacked consistency in their responses, probably due to the scatter generated in density-flow relationships as individuals integrated a range of hydraulic conditions during their streambed movements under disturbance (Lancaster and Belyea 2006).

In the astonishingly few instances where it has been explicitly examined as a flow index (Section 7.1), discharge reduction on the day of sampling has also shown mixed degrees of influence in several other studies addressing the effects of natural and artificially reduced flows on invertebrates. No distinct patterns of taxon response to discharge reduction could be elucidated based on an index of instantaneous abstraction for numerous U.K. rivers subjected to varying kinds and degrees of water abstraction (Castella *et al*. 1995). With periodic dewatering with diversion in a perennial reach of Tai Po Kau Forest Stream, Hong Kong, discharge at time of sampling (estimated from stream width) was significantly correlated with certain taxa, for instance positively and negatively with trichopteran and coleopteran densities, respectively (as well as with species richness) (Dudgeon 1992b); unfortunately, as streamflow records were not available the potential influence of the stream's natural history of flow disturbance could not be gauged.

In the present case, the families implicated, the number showing significant relationships with Q_{inst}, and the direction of response for each family, as compared with reactions under natural flows, varied noticeably

among rivers. Although the various trends could be readily matched with previously identified, dominant invertebrate redistribution pathways, families reacted less to the artificial discharge reduction *per se* and more directly to flow-mediated transformation of the immediate patch environment. As Davis and Barmuta (1989, p. 280) noted, "Not all benthic species will select habitat purely on the basis of flow." Moreover, as discharge changes, key correlates of habitat quality also change at the spatial scale relevant to benthic invertebrates (Poff and Ward 1991). Invertebrate responses to experimental dry-season discharge abstraction, by on average 89-98% for a month in three New Zealand streams, were also more obviously related to flow-mediated changes in habitat, including chemistry, and the relative sensitivities of invertebrates to such changes, than to the actual discharge magnitude (Dewson *et al*. 2007a, b). Explicit relationships were not documented, however, and links to flow history could not be established due to the absence of long-term flow records. On four other N.Z. streams, riffle communities, as well as some individual taxa, from above and below abstraction points removing up to 98% of discharge were separated in ordination space along an axis that correlated negatively not only with discharge, but additional abiotic factors (Dewson *et al*. 2003).

Diversity and instantaneous discharge

Similarly, invertebrate diversity indices yielded limited evidence of discharge at the time of sampling directly shaping invertebrate response, with few trends of any significance (as also supported by broad diversity trends in Section 7.6). Relationships were indistinct or lacked consistency from river to river, as well as across biotopes, for all diversity measures examined, though within individual rivers the directions of response based on diversity showed improved consistency. More importantly, where diversity-Q_{inst} trends were apparent, their varied directions reinforced invertebrate patch dynamics under artificial flows. The variability in indices such as Shannon-Wiener diversity also suggested strongly localised influences of patch conditions on the benthos, as borne out by responses of invertebrates to habitat patch metrics below. On their own, diversity measures specifically for riffles also tended not to be useful mirrors of immediate response to instantaneous discharge. The sole generalisation possible across multiple rivers and diversity measures was a weakly significant increase in the total numbers of individuals inhabiting riffles with declining Q_{inst}, representing a switch in response direction from that under natural discharges. Increases in densities with low flows, often also for riffles, have been documented in other assessments of invertebrate response to disturbance, but not necessarily explicitly correlated with discharge magnitude (Gore 1977; Ladle and Bass 1981; Extence 1981; Canton *et al.* 1984; Wright and Berrie 1987; Armitage and Petts 1992; Dudgeon 1992b; Castella *et al.* 1995; Pollard *et al.* 1996; Rader and Belish 1999; Ledger and Hildrew 2001; Suren *et al.* 2003; Dewson *et al.* 2003, 2007b; Section 7.1.3).

Whether in the context of natural or anthropogenically altered flows, the potential for direct daily discharge-diversity relations to adequately characterize disturbance has been variable in flow studies elsewhere. A strong relationship between total number of individuals and discharge was found, and attributed to changes in wetted bed area and associated habitat diversity, for invertebrate communities experiencing disturbance

due to multiple periods of severely reduced flows with drought, in the perennial Little Stour River, U.K. (Wood *et al.* 2000). Discharge was one of the dominant factors explaining variation in abundance and taxon richness, primarily at family-level, for 51 sites on 22 naturally diverse British rivers that represented a wide range of abstraction effects (Armitage and Petts 1992). Interestingly however, the lack of adverse impacts of flow reduction typically observed for the upland streams was attributed to their comparatively higher within- and between-year flow variability and hydraulic heterogeneity than lowland sites. It was postulated that the invertebrate fauna might be well adapted to the resultant extreme conditions involving marked losses of wetted habitat. The same rationale was proposed in the study by Castella *et al*. (1995) of 22 U.K. rivers of differing flow regime variability subjected to water abstraction over two summer periods, where no distinct patterns of response could be elucidated among a wide range of invertebrate taxa. Even though discharge was one of the environmental variables found to be most closely linked to flow reduction effects for a subset of rivers of the same basic biophysical type, responses remained limited and inconsistent. Although invertebrate total abundance and richness did not vary significantly spatially above and below a flow regulation structure in Mill Stream, U.K., they did seasonally, with discharge, along with depth and distance from the main River Frome, exerting the strongest influence on family abundances (Armitage and Pardo 1995). More apparent than in the current instance, but addressing a longer time period of discharges below Q_{95} with drought, strong correlations were found between dry-season discharge and benthic diversity indices, including Margalef's richness, Pielou's evenness and Shannon diversity, in Strouma River, Bulgaria (Dacova *et al*. 1992). However, an inconsistency in trends with discharge reduction, as well as better fit relationships for indices in combination than singly, were reported.

Based on the present study, not only measures of the magnitude of daily discharge as a disturbance index, but also of benthic invertebrate diversity appeared limited in describing meaningful low flows in the short-term. Invertebrate responses were clearly contingent on multiple environmental factors, as also highlighted by Lancaster and Belyea (2006) and Konrad *et al*. (2008), with few well-defined relationships and of high variability between the single hydrological index and individual biotic indices. Response to reduced discharges was more readily inferred from invertebrate relations with other abiotic factors mediated by flow, such as hydraulic habitat character and dynamics. This supported Lancaster and Belyea's contention (2006) that an approach exclusively focused on direct discharge relationships seldom reveals the underlying mechanistic or functional basis of response. To adequately represent the influence of reduced streamflow on invertebrates in the short-term, it was therefore essential to incorporate abiotic factors that effectively integrated the immediate, indirect effects of the disturbance spatially and directed the nature of many of the responses observed, as well as to explore hydrological indices operating at other temporal scales. While not explicitly addressed here, the potential for influence of near-term antecedent flows was apparent in this regard, as emphasised in a number of other ecohydrological studies (Biggs and Close 1989; Feminella and Resh 1990; Boulton and Lake 1992a; Feminella 1996; Winterbottom *et al*. 1997; Wood *et al.* 2000). Ward (1976, p. 243) observed that "the flow history of the immediately preceding period may be more important than the instantaneous flow at the time of sampling". In the frequently drought-disturbed Little Stour R., the

mean daily discharge the week prior to sampling (as well as DWF, i.e. average of seven consecutive days of lowest flow in the previous 12 months) was moderately to highly correlated with invertebrate dry-season abundances (Wood *et al.* 2000).

8.8.4 Relating invertebrate response to multiple abiotic measures of low-flow disturbance across temporal scales of influence

Immediate flow-habitat conditions and invertebrate response

The 'immediate flow' window, encompassing the flow-disturbance timeframe of days to weeks within the dry-season, clearly bridged scales of hydraulic to hydrologic influence. This area of transition in the temporal continuum from instant flow-mediated hydraulic habitat conditions to long-term hydrological regime, though poorly known (Biggs *et al*. 2005), demonstrated high potential to characterize invertebrate assemblage response to low-flow disturbance. In an illustrative example of this aspect of disturbance, a spectrum of variations in velocity formed the basis of a conceptual model linking scales of flow variability to New Zealand river structure and functioning (Biggs *et al*. 2005). The model spanned 'hydraulic' flow variations that affected processes of uptake of inorganic nutrients and food at temporal scales finer than days, and 'hydrological' scale flow variability (months to years) linked to drag-disturbance, with biomass dislodged and lost due to high velocities, and bed sediments mobilised.

Although playing central roles in the immediate reactions of the benthos to low-flow disturbance, particularly for individual flow-sensitive taxa at small patch scales, the advantages of moving away from a reliance on single hydraulic attributes of habitat quality or flow indices, to a combination of these and other abiotic factors, were evident. Particularly, as a result of patch environments being at different stages of disturbance across the riverscape and invertebrates using hydraulically marginal conditions to tolerate short-duration low flows, the resolution was lacking to comprehensively portray disturbance responses of flow-impacted assemblages exclusively on the basis of hydraulic quality. Consequently, characterization of relevant flows for assemblages across a gradient from natural to unnatural low-flow disturbance, at least for riffles (the biotope studied in depth), was markedly more effective with the inclusion of biotope-specific patch metrics reflecting the actual availability of preferred habitat in terms of wetted surface area and cross-channel width and perimeter, in addition to key hydraulic variables. The latter indices delimiting riffle environments encompassed Fr, VD_{ratio}, NBV, depth and, at severe low flows, relative exposure. Even slight changes in water quality influenced invertebrate responses to low-flow disturbance, although the specific chemical parameters varied in each instance. Commonly, conductivity was most influential, lending support to earlier observations that flow reduction, especially down to levels associated with local patch isolation, exerted secondary effects on this aspect of environmental quality (Section 5.3). Instantaneous discharge expressed as a flow percentile, and an assortment of other abiotic variables, were also of limited influence. In only a few instances could the closest associations with biotic diversity be ascribed to a single abiotic factor at low flows, and then those implicated were chiefly hydraulic indices. Whilst there were similar responses for those taxa previously identified as flow sensitive, a pronounced lack of consistency across sites

and combinations of variables along the same disturbance axis suggested the approach was of less use for individual taxa than say strictly hydraulics-based relationships.

For the perennial rivers of this study, achievement of the best-fit in characterizing meaningful low flows for invertebrates during the short-term disturbance phase required the integration of more proximate hydraulic habitat and chemistry descriptors with discharge indices. Although there appeared to be few other directly comparable studies, the multiplicity of invertebrate responses to discharge and related altered abiotic conditions gleaned from a wide array of low flow studies (Sections 7.1 and 8.1) supported this view. A combined flow-habitat index was considered a more effective way of quantifying changes in riffle habitat quality during low-flow disturbance, that might exert an influence on invertebrate assemblages independent of any due to discharge alone, during a survey of the effects of relative flow permanence on the benthos of Coosa River tributaries, U.S.A. (Feminella 1996). Boulton and Lake (1992a) reached a similar conclusion in studying the intermittent Lerderderg and Weerribee rivers, Australia, where no single environmental variable adequately differentiated among five flow phases identified at various sites. Each phase and the invertebrate assemblages associated with it were characterized by a complex combination of discharge and historical flow events, hydraulic habitat and water chemistry. They deduced that models of community structure should incorporate flow disturbance history, seasonal and habitat (equivalent to 'biotope' in this context) variations, physiochemical factors, and biotic interactions.

Several approaches for establishing environmental flows for invertebrates have gravitated towards variously integrating flow indices with multiple biophysical factors, and in rather innovative ways (see for instance: Jones and Peters 1977, cited in Dunbar *et al*. 1998; Docampo and De Bikuña 1993; Petts *et al*. 1995; Choy *et al*. 2000; Buffagni 2001; O'Keeffe *et al*. 2002; Dunbar *et al*. 2004; Section 8.1.3). For example, an empirical model was generated from relationships between invertebrate BMWP scores for multiple River Glen sites and the best-fit attributes, Q_{95} divided by average channel width, flow type (a composite variable of average wetted width as a % of channel width and the proportion of the reach with visible flow), percentage cover, and a composite chemical score (Petts *et al*. 1995). It was then used to determine a recommended flow of Q_{99} to maintain the 'minimum acceptable character' of the aquatic invertebrate community. Notably, relationships were improved when hydraulic habitat conditions under the extreme low flows at the time of the field survey were used, as opposed to longer-term average conditions.

Characterizing low-flow disturbance using monthly flow indices

When connections were sought between invertebrate taxa and the natural history of flow disturbance to which they had been exposed at a roughly monthly window, a wide range of 15 monthly hydrologic indices previously identified as potentially relevant (Chapter 4) were strongly influential. There were numerous (73) positive and negative relationships with the densities of 22 of the 32 most common invertebrate families at natural low flows, although with only nine highly significant. Disproportionately more of the responses to monthly flow characteristics were negative and sometimes consistently so for all families, as found for

monthly flow volume and monthly average discharge. Speculatively, this pointed to invertebrates generally being seasonally adapted on the basis of their flow histories to respond favourably to lower and more stable flows during the summer period, as might well be anticipated. Solely monthly flow variability (CV) appeared ecologically relatively unimportant for those families common in the dry season. In contrast, the same index exerted positive and negative limits on benthic invertebrates for six different biotic measures in United States rivers, but across the western region with its diverse flow regime types (Konrad *et al*. 2008). A similar number of other hydrologic indices to that of the current study, characterizing streamflow at multiple temporal scales, were also biologically influential at the 111 U.S. stream sites, based on strong associations with 14 of an original 157 invertebrate metrics for predominantly riffle assemblages at low flows. Of those indices, flow variability for daily and monthly temporal windows was associated with the greatest number of different assemblage measures, showing limits on all major invertebrate metrics bar two. In an assessment of the relative influence of 48 different flow indices in explaining variation in invertebrate communities with low-flow disturbance, due to multiple periods of severely reduced flows with drought in the perennial Little Stour River, U.K., flow indices representing a seasonal flow window were in fact rejected in favour of monthly flow indices considered more representative of the actual disturbance timescale (Wood and Petts 1994, 1999; Wood *et al.* 2000). Overall, 18 flow indices were particularly ecologically relevant, with best-fit correlations with some measure of assemblage composition (Wood *et al.* 2000). Monthly mean discharge, followed by minimum and maximum monthly flows, were the strongest predictors of macroinvertebrate abundances late summer, based on ten variables representing various aspects of assemblage composition (total number of individuals, number of families and species, and individual species' abundances).

Interestingly in the present study, when expressed as a monthly flow percentile, instantaneous discharge was the most influential flow variable within a monthly temporal window, closely followed by the monthly median seven-day low flow (Q_{7dLow}) and monthly maximum discharge (Q_{max}), effectively encompassing the full range in magnitude of monthly low to high flows. Monthly minimum (Q_{min}), and median flows (Q_{50} - which defines the low-flow envelope; Smakhtin 2001) were also detectably linked to invertebrate response. Certain families, including the Elmidae, Leptoceridae, Notonemouridae, Hydroptilidae and Oligochaeta, exhibited higher densities at low values of monthly indices such as Q_{min}, median Q_{7dLow} and Q_{50}. This result suggested they might therefore possess enhanced tolerances for naturally lower dry-season flows. In contrast, the Heptageniidae in particular, as well as two other ephemeropteran families (Baetidae and Leptophlebiidae), Hydropsychidae, Acarina, Philopotamidae, Limnichidae and Pyraustidae were among those taxa that showed the converse pattern, responding positively in terms of mean densities to monthly indices reflecting naturally elevated flows over the dry season. Though taxon relationships with specific flow indices remain uncommon in the literature, Heptageniidae are a family reportedly intolerant of very low flows, yet tolerant of higher flows (Ward 1976; Ward and Short 1978). Similarly, trichopterans including the Hydropsychidae (Larimore *et al*. 1959; Ward and Stanford 1979; Hauer *et al*. 1989; Growns and Growns 2001), and Baetidae (Larimore *et al*. 1959; Ward 1976; Ward and Short 1978; Lillehammer and Saltveit 1984b; Saltveit *et al*. 1987; Brittain and Saltveit 1989; Castella *et al*. 1995; Rader and Belish 1999; Wood *et*

al. 2000), are known to be low-flow sensitive groups that respond in varying ways to hydrologic alteration according to the type of regime change and the species involved.

Although standard low flow percentiles (Q_{75} to Q_{99}) were not particularly ecologically relevant at monthly scale, with responses for only a few taxa (e.g. Acarina, Athericidae and Libellulidae), Q_{95}, together with monthly median Q_{7dLow} and monthly Q_{max}, were weakly influential in structuring invertebrate assemblages. The index Q_{95} was previously demonstrated to be one of the useful indices for river hydrological characterization (Chapter 4). Although Q_{95} and several such percentiles are widely used internationally at both monthly and annual time steps in environmental flow studies, this has generally been without much evidence of their ecological meaning for aquatic biota (Tharme 2003; Pyrce 2004; Arthington *et al*. 2006; see also Sections 4.1.2 and 1.5). In certain instances though, an effort has been made to derive low flow percentiles as recommended flows on the basis of invertebrate and associated abiotic responses to flow alteration. A Q_{99} minimum flow for maintaining the invertebrate community of the River Glen, eastern England, was based on such an integrated ecohydrological model (Petts *et al.* 1995). Within the U.K. CAMS process, the ecological sensitivity of a river system to flow change and hence, the percentage of natural Q_{95} recommended as an environmental flow for water permitting, have been based on a combined scoring system that considers, among other elements, measures of physical habitat condition and benthic invertebrate composition (Dunbar *et al*. 2004). Under England's procedure for licensing surface water abstractions, minimum flows have been set as Q_{95} and Q_{98}, for sensitive and less sensitive rivers, respectively, based on an environmental weighting system for different river types that incorporates the tolerances to flow reduction of multiple invertebrate taxa (Bragg *et al*. 2005).

As with the characterization of immediate disturbance effects in the present study, monthly flow indices that described differences in site flow histories were really most influential in structuring assemblages when in combination with metrics reflecting actual reach conditions during the low flow events. Importantly, these flow indices then assumed a lesser influence than the latter abiotic disturbance measures. Moreover, while the same monthly flow indices were implicated, Q_{95} was more prominent than either Q_{75} or monthly maximum discharge at this time step. In contrast, the median Q_{7dLow} and instantaneous flows were of limited influence once other abiotic factors were included. The descriptors of altered physical habitat to which invertebrates most consistently responded (in terms of monthly mean densities) were: a measure of the amount of wetted habitat available (that is, total wetted surface area and cross-channel width); its degree of connectivity within the streambed; and whether or not it provided flowing-water conditions. While physical habitat measures comprised a small cohesive group, a more diverse assembly of water quality variables, several of which are well established to exhibit relationships with low flows (Dallas and Day 1993; Malan and Day 2002b; Nilsson and Renöfält 2008; Section 5.1.1), variously affected assemblage response at reach scale. Generally, EC (and certain salts) and nutrients were key constituents within that group, with the former parameter already shown to be of influence in the context of immediate disturbance. Responses to disturbance brought about by flow reduction have been demonstrated to differ depending on differences in

the sensitivity of invertebrate assemblages to varying water quality, notably in terms of ambient nutrient levels (e.g. Castella *et al*. 1995; Suren *et al*. 2003; Dewson *et al.* 2007a). Moreover, low flow events are known to exacerbate the adverse effects of other stressors on invertebrates, central among these being changes in water chemistry and hydraulic habitat, leading to potentially complex and not necessarily consistent ecological responses to such events over time in any specific location (Boulton 2003).

Influence on invertebrates of long-term flow history based on annual flow indices

Events defined by hydrological indices reflecting an approximately monthly (or within-season) timeframe appeared to condition natural invertebrate response to dry-season flow disturbance more than did annual indices, purely on the basis of the far higher total number of significant relationships encountered in the former instance. However, a similar total number of families was implicated at monthly and annual scales. The fact that individual low flow events tend to be of longer duration than high flow ones (Poff 1996) may in part explain this trend. Konrad *et al*. (2008) similarly reported that of a diverse suite of biologically meaningful hydrologic indices, measures of daily and monthly flow variation were associated with more invertebrate assemblage measures than flow indices of other temporal spans, and thus potentially especially useful as benchmarks for ecological flow management in the Western U.S.

More than was the case at monthly scale, certain of the annual flow indices identified *a priori* as potentially ecologically relevant (Chapter 4) bore little influence on abundances of any of the dominant families in the different perennial river reaches. Notable among these were several indices generally considered or expected to be influential from a low flow perspective based on some ecohydrological studies to date, namely the annual Q_{50}, Q_{80}, median Q_{7dLow}, and Q_{min} and its corresponding variation (expressed as CV). Still, twenty of the 32 most common invertebrate taxa across the rivers were responsive to a total of 21 different annual measures of natural flow-disturbance history, with numerous (41) influential trends identified between flow variables and individual families. The lack of significant connections between the other invertebrate families and annual descriptors of flow history did not necessarily mean that they were generalists responding principally to environmental factors other than flow, though this constituted one plausible explanation. Rather, for a number of families the relation with disturbance history was simply more strongly apparent for monthly than annual flow indices. This result was corroborated by similar ecohydrological studies where varied measures of assemblage composition responded in different ways to the same flow index or to flow indices reflecting a range of disturbance time steps (Feminella 1996; Clausen and Biggs 1997; Ruse and Davison 2000; Reiseng *et al.* 2004; Monk *et al.* 2006, 2007; Konrad *et al*. 2008). Further, it confirmed Whittington's (2000) observation that if a taxon does not respond to a particular flow index, it does not necessarily mean that the index is not relevant for other taxa in the same assemblage.

Certainly, some families appeared more markedly influenced by annual measures of flow history than others, with Caenidae, Hydraenidae and two odonate families the most responsive overall. The different combinations of annual hydrological indices to which families responded most provided an indication of the

long-term flow disturbance patterns conducive to their persistence and to which they might best be adapted. A number of families, among them the Teloganodidae, Hydraenidae and Corydalidae, responded positively to indices reflecting higher degrees of long-term flow predictability and stability, both annually and during the peak of the dry season (e.g. Colwell's overall and low flow predictability, *P* and *P*-low, respectively, and constancy, *C*). Concomitantly, they showed negative relationships with measures of annual and peak dry-season flow variability (and similar measures), annual CV and CV Dry, respectively, for the same timeframes, as well as with high flow indices. Similarly, caenids exhibited elevated mean densities at higher values of most low flow percentiles, but were negatively associated with flood events and their year-to-year variability. As an example, these trends point to a possible predisposition by such families for reliable and not extremely low dry season flows, coupled with fairly stable periods of moderate high flows.

Trends in the densities of several common species were also positively associated with long-term flow disturbance described as a gradient of streamflow permanence at low flows (incorporating Q_{50}, and minimum discharge and mean wetted riffle area at summer baseflow), across multiple tributaries of the Upper Coosa River, U.S.A. (Feminella 1996). Similar to the present study, this was presumed due to increased hydrological stability and availability of suitable habitat for rheophilic taxa. For instance, Ephemeropteran-Plecopteran-Trichopteran (EPT) richness showed the strongest, positive relationships with flow permanence of all assemblage attributes, with *Cheumatopsyche* and *Chimarra* mainly restricted to the most flow-permanent stream, and the mayfly *Stenonema* and simuliids showing increasing densities with increasing stream permanence. In contrast, a significant negative relationship was found between summer permanence and the percent of non-insect taxa. At certain of the sites examined along the low-flow altered River Glen, the range of invertebrate taxa showing significant hydrologic preferences, based on their relationships with indices reflecting flow disturbance history, differed markedly from that of other locations (Bickerton 1995). Certain families, including Leptophlebiidae and Rhyacophilidae (predatory caddisflies with a preference for high velocities) were more frequently encountered in higher-flow dry seasons, while Hydropsychidae surprisingly appeared not to show significant flow preferences at any sites. Where summer low flow regimes were affected by water transfers, a relatively high number of taxa were more frequent in low-flow summers characterized by a seven-day low flow threshold and thus, by implication, more tolerant of associated low flow conditions.

Using relationships between LIFE scores, representing an integration of the flow-related requirements of entire benthic assemblages, and a vast suite of hydrological indices reflecting flow disturbance history from annual down to finer temporal windows, it was possible to document the most influential characteristics of the hydrological disturbance regime affecting invertebrates across multiple river types in the U.K. (Extence *et al*. 1999). For example, for the Waithe Beck, a subset of hydrologic indices with best-fit relationships with invertebrates could be identified as potentially the most important from among 177 significant and only eight non-significant correlations obtained between LIFE scores and annual to daily flow variables. The existence of important drought-induced low flow thresholds could also be highlighted based on the

deterioration of the relationship between LIFE scores and key flow variables. Addressing an equally wide range of river flow regimes and diverse measures of invertebrate composition, Konrad *et al*. (2008) also showed differences in the degree of association of taxa with various hydrological descriptors of disturbance history, as well as differences in the relative positive and negative influences of different flow measures, across annual, monthly and daily time steps. In their study, every invertebrate index showed a clear limit associated with at least one flow characteristic and, while not an issue investigated in this thesis, central responses to flow (*sensu* Lancaster and Belyea 2006) were relatively less sensitive than upper or lower limits of invertebrate response to the particular flow characteristics. Invertebrate indices found to be commonly associated with multiple flow metrics were the relative abundance of Plecoptera, followed by the total number of non-insect taxa and relative abundance of intolerant taxa (i.e. sensitive to perturbation). Whilst invertebrate abundance and richness had fewer limits in relation to hydrologic metrics, those detected were linked to a wide range of hydrologic characteristics.

As also found in the present study, the direction of invertebrate metric responses was not consistent across all flow indices (Konrad *et al*. 2008). For example, the relative abundance of plecopterans increased with general long-term flow variability at the intra-annual scale, but decreased with inter-annual low flow variability (CV_{min}) and daily flow variability (as % daily change in discharge). Closely related invertebrate assemblage measures exhibited similar responses, however, while complementary groups of invertebrate indices responded predictably in opposite directions. Of the flow indices examined, median annual mean discharge was not particularly influential, but at the other end of the temporal scale, various components of invertebrate assemblages distinctly responded to daily flow variability. Although the low flow indices differed from those of this study and also did not necessarily match temporally, they similarly exerted influences on invertebrate assemblages in the long-term. Baseflow recession rate, median annual minimum daily discharge (Q_{min}) and the CV of annual minimum discharge (CV_{min}) were each variously associated with several biotic metrics. As for timeframes in the order of days to weeks, invertebrate response was shown to vary on the basis of antecedent flows over longer periods of disturbance history, with multiple invertebrate assemblages responding to hydrologic indices reflecting conditions 100 days prior to invertebrate sampling, and with fewer but similar limits of invertebrate response apparent for flows 30 days antecedent (Konrad *et al*. 2008).

Discrimination among ecological assemblages on the basis of hydrological variables has been considered potentially more difficult in a region characterized by narrow hydrological variation (Poff and Allan 1995). In the current study, all perennial rivers came from the same hydroclimatic region and were of the same regime type (Chapters 2 and 4). Hence, although differences in low flow regime were discernable across the sites, flow variability was relatively narrow overall. This factor may well have restricted the extent to which invertebrate response to low flows among sites could be identified and adequately characterized. Generally speaking, however, flow regime predictability (*P*) and constancy (*C*) remained fundamental attributes of the long-term pattern of natural disturbance to which the different invertebrate assemblages distinctly responded.

As influential were combinations of the annual low flow index Q_{95}, with annual average and median discharge and high flow magnitude (viz. Q_5 and annual volume). Of some additional bearing as long-term descriptors of flow disturbance were the low flow variables, MAM, Q_{99} and Q_{90}, as well as flow contingency (*M*). For 34 river sites across the mid-western U.S., fish assemblage groups, ecologically defined based on functional measures of species traits for 106 species, similarly responded to a flow stability-variability gradient, from rivers with a high CV of daily flows and moderate flood frequency, to more stable streams with high daily flow predictability (*P*) and stable baseflows (Poff and Allan 1995).

In a more general characterization of ecologically relevant flows for invertebrates across an array of 83 N.Z. river sites, predominantly employing annual flow indices that captured general, high, and to a lesser extent, low flow regime features, benthic density showed significant correlations with 30 of the 34 flow indices examined (Clausen and Biggs 1997). Several of these flow indices were similar to those for which distinct responses were evident in this study. Further, some measure of flow variability and predictability, generally flood disturbance frequency or relative low flow variability, was significantly related to most biological variables. Total number of individuals particularly, showed a significant negative correlation with the low flow indices, Q_{90} and MAM (also influential in this study), as well as with measures of flow stability such as constancy. Conversely, assemblage metrics tended to increase with increasing flow variability, as indicated by CV and skewness. Interestingly, a principal-components based combination of hydrological variables did not provide stronger relationships than single indices. As for the present study, whilst results of a study of 83 U.K. rivers, in which relationships were modelled between macroinvertebrate community metrics at family level and 201 flow regime descriptors, compared favourably with those of Clausen and Biggs (1997), the flow indices for predicting invertebrate response differed (Monk *et al*. 2006). Similarly though, invertebrate communities responded to many of the potentially ecologically relevant monthly and annual flow variables assigned to major flow regime attributes (Section 1.4.2, Table 1.2), as reflected over a multi-year period by LIFE and, to a lesser extent, ASPT metrics (Monk *et al*. 2006). For a model encompassing all sites, the strongest invertebrate response to flow history, described by LIFE score, was with median annual flow. Flow variables that reflected flow regime magnitude (i.e. magnitude of monthly water conditions, and magnitude and duration of annual extremes) consistently resulted in the strongest relationships with invertebrate community metrics for all sites. It was especially apparent for 'low flow regime' composite classes of hydrograph magnitude and shape that rivers of different hydrological regime type supported significantly different invertebrate assemblages. Unlike the present study and that of Konrad *et al*. (2008) (but cf. Clausen and Biggs 1997), for the various rivers Monk *et al*. (2006) examined, one or two of the array of flow indices typically sufficed to explain a significant proportion of the variance in assemblage structure.

Annual flow variables with lesser roles in dictating natural patterns of invertebrate composition and disturbance response in the present study encompassed all of the main regime components, and included descriptors of low flows, floods, general flow conditions and overall regime variability. Although the low flow indices median Q_{7dLow} and Q_{80} remained of as little influence for entire assemblages as they had been

for individual families, it is noteworthy that the former index appeared more relevant at a monthly time step. Interestingly, while Q_{50}, as a measure of general flow conditions, strongly influenced benthic assemblages overall, as also found by Clausen and Biggs (1997) and Monk *et al*. (2006), it did not emerge as particularly influential for any individual families. Average annual discharge, similarly influential in flow disturbance response at the scale of the entire assemblage, only showed distinct negative correlations with a few families. The Chironomidae was not one such family, unlike in the long-term Thames River ecohydrological study, England, where 19 chironomid taxa (including genera common to the present study) clearly responded negatively or positively in densities to mean annual discharge (Ruse and Davison 2000). While connected with the response to disturbance of certain individual families, for entire assemblages overall flow regime variability (annual CV), as well as high flow indices reflecting the annual maximum discharge and 1: 2-year return period flood, also were less obviously relevant in the current study. Likewise, across multiple sites on the Taieri River, N.Z., discharge CV and variance, and flood frequency, did not appear to strongly influence invertebrate assemblages, at least in terms of taxon richness (Townsend *et al*. 1997a). In contrast, differences in the composition of two major invertebrate community groups were attributable to major variations in flow variability across other N.Z. rivers, with distinct correlations reported between the annual CV of flow and various river biophysical characteristics (Jowett and Duncan 1990).

In this study, it was striking that invertebrate low-flow disturbance responses were not only naturally conditioned by patterns of overall flow variability and low flow events, but also by each river's high flow history. For longer-term temporal windows especially, this suggested that low flow indices alone or in combination with more general flow descriptors were insufficient to characterize meaningful low-flow disturbance events for the benthos. This finding is supportive of the ranking by Poff and Ward (1989) of the major temporal components of hydrological variability according to their relative importance in defining the physical template of a river where, apart from degree of intermittency, flood frequency and predictability, as well as overall flow variability, were recognised key factors. Whilst high flows have often been demonstrated to be the dominant architects of disturbance for benthic invertebrates, for instance exerting short- and long-term effects on the patchiness of their local distributions (Matthaei and Townsend 2000; Sections 1.4.4 and 8.1.3), their comparative influence during natural dry periods, relative to that of low flow factors, has seldom been ascertained.

Nonetheless, in an illustrative example, significant associations of invertebrates with flow indices were found for most months of the year in the intensively low-flow perturbed Little Stour River, but rather than low flow measures it was indices of high flows, or the absence of such flows four to seven months prior to sampling, that were most important in characterizing the late summer invertebrate community (Wood *et al.* 2000). This result similarly highlighted the important role flood events, as well as antecedent flow conditions, can play in invertebrate dry season responses to flow disturbance. Conversely, for numerous sites on the English River Glen, distinctive invertebrate assemblage and taxon responses to a disturbance history of flow abstraction and drought were only apparent for the low-flow season. Then, they were principally related to

the low flow indices, April mean daily flow and summer seven-day average discharge (in the year of sampling and the preceding one), rather than to the wet-winter seven-day high flow (Bickerton 1995). In an assessment of which of 34 hydrological indices were most influential in characterizing the natural disturbance regimes for benthic invertebrates of numerous New Zealand rivers, even though the communities were of the late dry season the frequency of floods three times higher than the median discharge was the most influential single flow index, alone accounting for up to 36% of community variance (Clausen and Biggs 1997). That there was still considerable variation remaining after invertebrate metrics had been related to hydrological regime underscored a need to incorporate additional variables to account for aspects of habitat other than those directly related to flow in characterizing the communities (Clausen and Biggs 1997) - as done in this thesis, but in the context of short-term artificial disturbance.

From the examination of annual, monthly and daily measures of flow history, it was evident that many but not all of the flow indices that were most effective in representing river hydrological character could be usefully connected to invertebrate response to flow disturbance in the immediate or longer-term, and hence, be considered truly ecologically relevant. The importance of selecting appropriate descriptors of invertebrate assemblage response to flow disturbance, given that various descriptors showed differing levels of response to a particular flow perturbation event, was plain (Miller and Golladay 1996; Englund and Malmqvist 1996). An array of multiple diverse hydrological indices, as well as of biotic measures describing assemblages, was required to comprehensively characterize ecologically relevant low flows for invertebrates in the context of long-term disturbance history. In this and other ecohydrological studies (Townsend *et al.* 1987; Jowett and Duncan 1990; Bickerton 1995; Clausen and Biggs 1997; Extence *et al.* 1999; Wood *et al.* 2000; Whittington 2000; Ruse and Davidson 2000; Growns and Growns 2001; Riseng *et al.* 2004; Monk *et al*. 2006, 2007; Konrad *et al*. 2008) it has been demonstrated that different invertebrate families and broader assemblage measures responded to different flow statistics, often with highly specific responses to particular indices. Moreover, as also encountered by Konrad *et al*. (2008), the responses of complementary invertebrate assemblage measures to flow indices were seldom redundant. Even flow variables that showed a fair degree of intercorrelation were not necessarily associated with the same sets of invertebrate assemblage attributes. While there was a core group of low, high and more general flow variables that were obviously more influential than others as central drivers of hydroecological variability, no single index or flow characteristic it represented was entirely responsible for effecting wholescale response by a benthic assemblage to low-flow disturbance. In the same way, across a wide range of U.K. river sites, while single hydrological variables were effective in accounting for much of the variation in invertebrate communities at individual river sites based on invertebrate LIFE scores, in some cases combinations of flow variables provided a more comprehensive description of the most influential factors (Extence *et al*. 1999).

No single set of indices consistently characterized low-flow disturbance across the multiple perennial rivers of this study, even though the systems were biophysically comparable, rendering it more difficult to resolve which attributes of a flow regime might be responsible for individual responses detected (Bunn and

Arthington 2002). Low flow-invertebrate relationships appeared site-specific even within the same system, across 45 sites on the River Glen, with responses most complex in reaches where a range of mesohabitats supporting high taxon diversity potentially responded differently to annual flow dynamics (Bickerton 1995). At the other end of the flow spectrum, in a flood disturbance study of the Kye Burn, New Zealand, it was similarly clear that the effects of local flow disturbance history on invertebrates were not always consistent across sites, even where those sites represented locations with contrasting geomorphologies, but along the same stream (Matthaei and Townsend 2000).

It was crucial in the current study to take into account each river's long-term hydrological disturbance history (Feminella 1996; Puckridge *et al*. 1998; Jorde and Bratrich 1998; Extence *et al*. 1999; McIntosh *et al*. 2008), even to be able to adequately address short-term variation in invertebrate response (Grimm and Fisher 1989; Boulton and Lake 1992a). In one insightful case, differences in the degrees and directions of riffle invertebrate response, with lesser reductions in the density and biomass of families such as Hydropsychidae and Chironomidae in the perennial upper Waihee River, as compared with neighbouring Iao Stream, were postulated to be the result of differences in flow regime characteristics between the two Hawaiian systems (McIntosh *et al*. 2008). Iao Stream exhibited a more variable flow regime (higher CV) with more frequent spates, but lower flow volume, mean, median and minimum daily discharge than the Waihee R., which therefore provided higher and more stable flow levels and habitat quality. Although it might be supposed that invertebrates of streams like Iao Stream, that have experienced lower natural flow minima and greater variability over their flow history, might be less susceptible to non-natural low-flow disturbances than the taxa of more constant rivers like the Waihee, the converse appeared to hold.

The various findings reported on here support earlier thinking that long-term disturbance histories may be more important than individual events in shaping lotic communities (Resh *et al*. 1988; Poff 1992; Riseng *et al.* 2004). Rivers exhibiting different flow characteristics might therefore reasonably be expected to respond biologically in potentially quite different ways to similar low-flow disturbances, as observed in this study even within the same basic flow regime and biophysical type. In this regard, there is little doubt that a great deal remains to be learnt regarding the differences in response of invertebrates to natural flow conditions within the realm of their evolutionary setting, as opposed to anthropogenic flow characteristics that may fall outside that context (Konrad *et al*. 2008). Understanding of the hydrological variables most influential in structuring invertebrate assemblages, and hence ecologically relevant, remains surprisingly limited. As highlighted by Wood *et al.* (2000) and Monk *et al*. (2006, 2007) there is a particular need to develop long-term ecological time series for comparison with descriptors of long-term flow disturbance to further validate river flow-ecology relationships. Thus far, ecohydrological studies have all too infrequently been structured from a flow disturbance perspective that explicitly encompasses different scales of hydrological regime history, and which incorporates multiple measures of the physical disturbance impact and the biotic response elicited. The adoption of such an approach in this chapter greatly facilitated the identification of low flows that could be considered ecologically relevant for benthic invertebrates.

9. LOW-FLOW DISTURBANCE AND INVERTEBRATE RESPONSE: SYNOPSIS, FUTURE RESEARCH DIRECTIONS, AND APPLICATION IN ENVIRONMENTAL FLOW SCIENCE

9.1 SYNOPSIS OF FINDINGS: LOW-FLOW DISTURBANCE AND INVERTEBRATE RESPONSE

9.1.1 Context

The intensification of hydrologic alteration and resultant degradation of freshwater biodiversity worldwide have necessitated a new and explicit focus on relationships between various attributes of the flow regime and ecosystem integrity, particularly when addressing environmental flows within river management. A wide array of more than 200 environmental flow methodologies has emerged over the past forty years, relatively few of which have been substantively underpinned by stream ecosystem theory. Recent advancements in holistic type methodologies, however, have heralded a new direction in environmental flow science more firmly rooted in contemporary river theory. That theory has necessarily evolved in tandem, with elements of hydrological, fluvial geomorphological and disturbance theories, habitat patch dynamics concepts, and ecohydraulics uniquely combining as the conceptual foundation of a new discipline - ecohydrology.

Ecohydrological research has expanded exponentially in recent years from this base, to support ecological flow management, with greatest emphasis placed on lotic response to flow-related disturbance. While the majority of studies have shown high flow events to be the chief disturbance agents in rivers, far less is known about the nature of low flows as physical disturbances or their ecological effects. This holds true for both natural and unnatural low flow events as drivers of benthic macroinvertebrate response in perennial rivers.

Thesis aim and hypotheses

In this thesis, the aim therefore was to identify and characterize ecologically relevant low flow events that constituted various degrees of physical disturbance to benthic macroinvertebrate assemblages of perennial rivers, by linking key flow indices with invertebrate responses to, and physical changes in, habitat conditions at low flows. It was hypothesised that detectable relationships exist between the composition of invertebrate assemblages and the flow-related quality and quantity of instream physical habitat, and these relationships can be used to identify characteristic responses of invertebrates to low flows. It was further postulated that there are degrees to which natural and unnatural low flow events constitute disturbances to invertebrates,

which are a function of assemblage composition, physical habitat conditions, and a river's characteristic hydrological regime.

The research conducted supported both hypotheses, though it proved difficult to extract generalisations regarding observed responses to short-term low flows, without using multiple lines of evidence over a range of spatial and temporal scales. Both the natural and extreme low flow events characterized in this thesis constituted pulse disturbances that elicited variable, but detectable changes in habitat availability and quality, to which benthic macroinvertebrate assemblages and individual taxa often responded subtly and in diverse ways. There was also a detectable gradient of invertebrate response to low-flow disturbance, even within biophysically similar rivers of the same flow regime type, influenced not only by natural hydrological variability, but also attributes of physical habitat, water chemistry, and invertebrate composition.

Methodology

The ecohydrological study was one of few empirical field-based, interdisciplinary experiments of the impacts of short-duration discharge reductions on multiple perennial rivers to date. The biophysically similar nature of the study sites and their flow regimes was demonstrated *a priori* through a pilot survey. An experimental, graded series of discharge reductions of approximately 36, 85 and 86% (each randomly assigned to a site) were implemented in the middle of the dry season, using temporary flow diversion weirs, in the largely natural, upper reaches of three of four perennial southwestern Cape rivers, South Africa; the remaining river acted as an overall control site. Manipulated flows at sites remained fairly constant in their magnitudes over the diversion period. Based on river low-flow histories, irrespective of their different proportions of natural flow, the artificial discharge reductions represented extreme low flow events not experienced over almost 30 years in any of the experimental reaches, in either magnitude or duration. Replicated sampling of physical habitat, water chemistry and benthic macroinvertebrates was conducted in upstream un-impacted (control, natural flows) and downstream flow-impacted locations during a midsummer two-month period of flow diversion, as well as before and after perturbation, on all rivers.

9.1.2 Low flow regimes: characterization and identification of ecologically relevant flow indices

Hydrological regime characterization, though seldom factored into ecological studies of flow disturbance, proved essential to place the extreme low flow events in the context of the long-term, natural hydrological disturbance histories to which the study rivers and their biota were adapted. Beyond sharing the same overall flow regime type, each river possessed a detectably different, natural low flow signature which, with differences in high flow configurations, made it possible to identify both a fine gradient of flow variability across sites, and flow events of greatest potential influence in characterizing invertebrate response to low-flow disturbance. Comparatively speaking, individual site hydrographs showed the following principal natural features:

- Experimental site of small size, subjected to the greatest discharge reduction (≥ 86%, far below the natural absolute minimum flow, AMF) - This site diverged most in natural hydrological character from the other sites, with lowest overall predictability, highest variability and lowest predictability of mid-dry season low flows, coupled with a flashy flood regime.
- Experimental site of small size, subjected to the second-highest proportion of discharge reduction (≥ 85%, far below AMF) - This site had the lowest overall and dry-season variability, most stable and predictable low flow regime, as well as a non-flashy pattern of high flows.
- Experimental site of moderate size, with the lowest degree of flow diversion (≥ 36% and at about or just below AMF) - This site had a moderately stable low flow regime, with low occurrence of very low flows, and was subject to large floods.
- Control site, of moderate size, experiencing entirely natural low flows – This site had the highest, but predictable, overall flow variability, low frequency of very low flows, and large magnitude floods.

Some 16 flow indices, comprising three basic groups, effectively differentiated among river hydrological characters, and were therefore of potential ecological relevance in terms of characterizing invertebrate response to low-flow alteration:

1. Low flow indices reflecting the magnitude, variability and predictability of very low flows, particularly mid-dry season - The discharge equalled or exceeded 95% of the time (Q_{95}) and the mean annual minimum flow (MAM) were important in distinguishing among the rivers. Also key were: coefficients of variation of annual minimum (CV_{QMin}) and dry season (CV_{Dry}) discharges, the median seven-day low flow (Q_{7dLow}), and other low flow percentiles (Q_{80}, Q_{90}).
2. High flow magnitude, frequency and variability indices - Key indices were the flow equalled or exceeded 5% of the time (Q_5) and an index of inter-annual variability of peak floods. The maximum annual discharge (Q_{max}) and flood of 1:2 year average return interval were also influential.
3. General regime variability and predictability, as described by: the annual coefficient of variation (CV); Colwell's predictability (*P*), and its components flow constancy (*C*) and contingency (*M*); and mean daily flow.

Daily flow indices were not necessarily correlated strongly with monthly or annual/inter-annual indices and revealed quite different aspects of flow regime character, underscoring the likely need to assess invertebrate response for various temporal windows of flow disturbance history.

9.1.3 Short-term effects of low flows on water chemistry

None of the short-term effects of natural and extreme low flows on river chemistry were pronounced or consistent across reaches, such that changes in water quality alone were unlikely to be a critical or overriding influence on invertebrate response. Chemical variables were, however, contributors to several of the relationships found to be most useful for characterizing ecologically meaningful flows for the benthos. Comparison of flow-impacted conditions with historical physicochemical ranges (underutilised in low flow

research) demonstrated that discharge reduction did not alter any chemical variables beyond long-term reference levels. Thus, the isolated subtle changes in water quality detected during discharge reduction experiments were of the same order as the effects of natural low-flow variation and probably within invertebrate tolerance limits.

Electrical conductivity (EC) was one of few variables that distinctly increased in response to discharge reduction, particularly with the loss of habitat connectivity that led to localised isolation of habitat patches. Reinstatement of natural flows served to restore water quality by flushing detritus that had accumulated in isolated pools or barely-flowing areas of the main channel from flow-impacted reaches. Algal assemblages proved more useful indicators of low flow conditions than water chemistry *per se*, with proliferations of filamentous green algae especially, linked to major reductions in discharge. Changes in algal growth and other ecological processes with flow reduction (e.g. macrophyte decay and detritus accumulation), probably influenced local nutrient dynamics, as well as food resources and microhabitat refugia for certain invertebrates.

9.1.4 Physical habitat dynamics at low flows

It proved critical to consider reach physical habitat within a nested geomorphological hierarchy, with the degree of low-flow disturbance effect and characteristics of habitat-discharge response differing depending on the spatial resolution at which physical habitat was examined. Natural variations in channel geomorphology and associated streambed heterogeneity among and within individual river reaches measurably affected the nature and strength of the low flow-physical habitat relationships detected, with attendant implications for invertebrate response.

Even with natural discharge fluctuations, there were detectable changes in all physical habitat variables examined that created conditions potentially less conducive for invertebrate persistence and might be considered at least mild short-term disturbances. Artificial flow reductions caused far more significant decreases in the overall living space for invertebrate assemblages, well beyond the bounds of natural variability, with commensurate declines in the spatiotemporal availability of wetted physical habitat and changes in the hydraulic characteristics, connectivity and landscape dynamics of habitat patches - equally critical factors in terms of their potential to profoundly alter benthic distribution patterns. Certain habitat descriptors from within the diverse range examined at multiple spatial scales were more flow-reduction responsive than others, and were typically within the group of most influential factors in explaining invertebrate-flow dynamics.

Channel-width discharge-habitat relationships

Discharge reduction to unnaturally low magnitudes (especially > 85% reduction) resulted in significant and consistent changes in simple, channel-width measures of wetted habitat and hydraulics:

- Severe decreases were recorded for: wetted perimeter and less so, wetted width; riffle and run average and maximum water depths and mean-column velocities; and total wetted patch length for riffle and run transects. Riffle sections had diminished considerably in extent with flow reduction mid-dry season, with the remaining wetted habitat already approaching a naturally stressful level for the benthos.
- Dramatic increases occurred in the cross-channel proportions of extremely shallow and/or extremely low velocity or non-flowing waters.
- In extreme cases, whole cross-section transformation occurred from predominantly riffle to shallow run, with substantial bed exposure and loss of flow types characteristic of riffles, or from run to pool-run.

Hydraulic biotopes - classification and flow related hydraulic characterization

The most insightful effects of low flows on physical habitat from a biological perspective were gained from an assessment of the flow-related hydraulic characteristics and dynamics of individual biotope patches within the streambed mosaic. The hydraulic biotope proved a robust and hydraulically meaningful patch unit at low flows.

- Hydraulic classification demonstrated that all eight biotope types encountered in the field, including the three biotopes studied in depth (riffles, runs and pools), retained their hydraulic distinctness across multiple rivers (though least so for riffles), and at natural and manipulated extreme low flows.
- Biotopes represented relatively discrete mesohabitat patch types, imparting a high level of confidence in them as potentially biologically relevant habitat units for invertebrates (as confirmed through faunal analyses). Naturally distinct differences among dominant biotope types, due to complex combinations of hydraulic and other biophysical factors, paved the way for invertebrate assemblage and individual taxon specificities for particular biotopes and associated hydraulic conditions.

No single hydraulic index sufficed to fully discriminate among or classify different biotope types at a single low flow or across discharges, with best classification results generally due to some combination of standard and derived hydraulic variables.

- Though Froude number (Fr, as an integrative index of turbulence) was fairly consistently the single best biotope descriptor overall, especially at extreme low flows, it achieved greatest discriminatory power in combination with other hydraulic variables, with near-bottom velocity (NBV) and water depth particularly influential. Additional useful descriptors were the substratum median particle size, velocity to depth ratio (VD_{ratio}), Reynolds number (Re), relative roughness (R_{rel}), relative exposure (RE), and a further turbulence index (TI).
- At natural low flows, individual biotope types were effectively characterized by different sets of hydraulic variables, with differences in hydraulic ranges and variability for each hydraulic attribute. Riffle and pool biotopes represented extremes of the hydraulic continuum, with limited overlap in hydraulics while, as envisaged, runs typically showed intermediate hydraulic characteristics.

- Riffles were best characterized by high Froude numbers, mean-column (0.6V) and near-bed velocities, velocity: depth ratios, and RE, coupled with comparatively low depths and high variability in hydraulic ranges.
- Pools, which encompassed a diversity of subtypes, consistently exhibited very low Froude numbers and velocities, predominantly low depths, and high relative exposure.

Discharge variation exerted an influence on biotope character:

- While hydraulic biotopes remained distinct entities across the spectrum of low flows examined, there was discharge-dependency in terms of their dominant hydraulic characteristics. Changes were most pronounced for runs and riffles, while pools retained much of their natural hydraulic character.
- The biotope response model for extreme low flows exhibited the strongest discriminatory power of all discharge-based biotope classification models developed, with classification correspondingly most successful. Success was principally due to Fr and R_{rel}, with lesser contributions from VD_{ratio} and Re.
- Different biotope types became more discrete in their fundamental hydraulic character at extreme low flows than under the full range of natural low flows, due to a combination of multiple shifts in hydraulic character, with potentially high ecological significance. This suggested that invertebrates needed to respond to complex hydraulic transformations while under low flow stress, and that hydraulic barriers to invertebrate inter-patch movement might be greatest at that time. Notably, biotope types showed weakest differentiation in the most hydraulically heterogeneous and hydrologically variable river reach, potentially lessening such barriers to invertebrate redistribution under the most severely reduced low flows.

Riverscape biotope mosaic - patch dynamics and diversity at low flows

Although there were natural differences in overall biotope composition under all low flow regimes across rivers, runs were the dominant biotope type by wetted reach area and remained so during artificially reduced flows, where they assumed a central role in the provision of flow refuges for invertebrates. Generalised biotope responses and thresholds of probable transition among different patch states were identifiable with discharge fluctuations, with common sequential changes in individual patch type occurring across multiple reaches:

- Discharge reduction below natural water levels resulted in sequential shifts in the proportional dominance in wetted area by different biotope patches, from higher energy (e.g. riffles) and/or deeper patches to lower energy, slower velocity and/or shallower biotopes (e.g. shallow runs, pools), often with quite different hydraulics from the original patches.
- Riffles transformed to run patches with decreasing discharge (sometimes also with increasing flow), while runs transformed into either riffles or pools, among other types. Pool patches did not transition to riffles (though some became runs), nor the converse, however, highlighting the strong divergence

between these hydraulic biotopes. Pools also showed the least diverse hydraulic responses to decreasing discharge, though differing degrees of isolation were a prominent feature of this patch type.

- The biotope sequence and discharge at which transformation to another biotope type occurred differed according to the starting (original) hydraulic character of each patch, as well as the complexity of local bed topography and habitat architecture, with direct bearing on the extent to which response to discharge alteration was detectable and its effect was felt by invertebrates.

Total wetted surface area was responsive to discharge fluctuation, with habitat shrinkage most pronounced with manipulated flow reduction to extremely low levels, though only distinctly for two of the three flow-impacted reaches. Changes in biotope proportions were therefore even more dramatic in highly flow-impacted locations, because they occurred within a reduced amount of wetted habitat and with a concomitant shift in hydraulics from natural conditions:

- All low-energy pool-like environments showed consistent and marked increases in availability, including in patch number and size, in response to decreasing discharge. Pools also became variously isolated within and along the river channels as discharges decreased, with implications of such losses of pool connectivity and potential flow refuges for invertebrates. Degree of pool isolation was a particularly useful flow-disturbance indicator, with the number and areal extent of isolated pools entirely without contact with flowing water highest at extreme low flows.
- Higher energy patches showed the expected converse trend to that of pools, of a decrease in reach proportions with decreasing discharge - a useful indicator of low flow-habitat response. Riffle area was particularly flow-responsive, making this biotope the most ecologically useful to monitor. Riffles declined in availability most dramatically of all biotopes, with remnant riffle patches scarce and small at extreme low flows.
- Runs did not show a consistent flow-related response in patch area, but while they became less numerous at lower flows they provided far larger areas of remaining habitat (albeit generally shallow and slow-flowing) than did riffles.
- Biotope diversity remained relatively high in terms of the number of different patch types over time and across sites, marginally decreasing with diminishing discharge; overall patch number showed no definitive discharge response.

Habitat patch connectivity and flow refuge availability

Under natural low flow regimes, changes in reach patch connectivity were limited, with little riverbed exposure. Habitat fragmentation became pronounced as flows were artificially reduced, however, with increased channel dissection leading to decreases in the number of flowing streambed sections, patch contraction and isolation, and increases in exposed streambed areas that were partially or wholly desiccated. Streambed structural heterogeneity proffered vital sources of protection to invertebrates from such flow-driven fragmentation with remnant unaltered or relatively hydraulically tolerable patches in the landscape acting as refuges from flow disturbance. Such considerations proved critical in addressing low-flow

disturbance effects on the biota, affecting the availability of suitable flow refugia at a time of high vulnerability. Knowledge of those patch types most susceptible to shrinkage or desiccation with flow reduction and their individual physical properties assisted with predicting the implications for invertebrates of a decline in or loss of particular habitat.

9.1.5 Direct benthic macroinvertebrate responses to low flows

Invertebrate responses to low flow dynamics, including artificial flow reduction, were far subtler and complex than the physical habitat changes detected, making it essential to adopt a spatiotemporally multi-scale approach to adequately understand response dimensions. Responses to flow disturbance were quite often river specific (i.e. there were distinct individual 'river signatures'), somewhat masked by natural variability, and with dependencies on local benthic composition, physical habitat character and dynamics, water chemistry, as well as short-term and longer-term hydrological disturbance histories. Comparatively few flow-invertebrate responses were consistent in trends or strength across sites, degrees of flow reduction or related physical conditions, or even biological metrics, precluding the identification of many generic direct responses to low flows.

Artificial reductions in low flow may not have represented a novel disturbance, given that they were coincident with natural low flows that had already induced physical and physiological stress. The limited overall impacts of the flow alterations despite their intensity, as well as the rapid recovery shown, likely in part reflected the life history traits and other modes of adaptation of perennial river invertebrates that have enabled them to persist under very low natural flows in their past. Despite these considerations, it was possible to identify several characteristic responses of invertebrate assemblages and individual taxa to short-term natural and unnatural low-flow disturbance, and at different scales.

Scope of flow disturbance and the biotope as a relevant patch unit

Extreme flow reduction exerted patchy and non-uniform disturbance effects in space and time on invertebrates across all reach landscapes and biotope patch types. As a result, there were not unexpected localised differences in the degree of influence where the low-flow disturbance was felt, with the first conclusive signals of perturbation effects emerging at the scale of assemblages from different hydraulic biotopes. Most evidence of altered invertebrate assemblage composition and diversity could be logically explained by dynamic redistribution of individuals among and within streambed patches, and pointed to a conclusion that invertebrate response is highly dependent on the spatial configuration and connectivity of different biotope patches and their individual patch characteristics.

The ecological relevance of the hydraulic biotope as a habitat patch unit was thus firmly established:

- Invertebrate responses to low flows across multiple scales showed that hydraulic biotope type appeared to exert as much of an influence on assemblage composition as discharge *per se*, confirming the

robustness of hydraulic biotopes not only in terms of their physical characteristics, but also from an ecological perspective.

- Specific invertebrate assemblages, families and species were associated with different hydraulic biotopes and associated microhabitats, and hence specific complexes of hydraulic conditions, at natural low flows, underscoring the powerful influence of the low flow regime through hydraulic factors.
- Certain taxa were consistently useful indicators of biotope type and hence, flow hydraulics, at natural low flows and thus potentially sensitive to flow reduction and in different ways. Demonstrable benefits were gained, in increased understanding of response to flow alteration, by using multiple invertebrate indicators and at varying levels of taxonomic resolution, with different invertebrate taxa showing varied responses to the same unit of low-flow disturbance. Different invertebrates were also found to be more useful flow indicators in different rivers, though with a few families showing more generic patterns of flow response.

Riverscape redistribution patterns of invertebrate response

Redistribution patterns were driven by availability and access to wetted habitat, configuration and connectivity of the patch mosaic, patch features, and changes in the hydraulic suitability of individual patches and microhabitats; findings firmly endorsed current theoretical models of riverscape patch dynamics and flow refugium use. Further, there was conclusive evidence that natural differences in the biotope affiliations and hydraulic tolerances of invertebrate taxa and hence, their degrees of flow tolerance, influenced their redistribution pathways.

Variations in assemblage composition at extremely low flows appeared to reflect invertebrate responses to shifts in the availability of different habitats, rather than solely tolerances to the events. Just as biotope patches sequentially underwent hydraulic transformation with progressive flow reduction, shifts in invertebrate assemblage composition, typically reflected by various diversity measures, occurred across the same biotope continuum, with species' responses (only Chironomidae were assessed) according well with those at family level. Coupled with this dynamic redistribution of the benthos across different biotope patches, there was evidence of within-patch redistribution down to the microhabitat scale of individual stone parts.

Invertebrates displayed several direct responses to extreme discharge reduction, with some taxa exhibiting multiple responses, depending on conditions within the affected individual patch compared with neighbouring habitat patches of the same or different types. Differences in the degree and direction of change (including from those found at natural flows) in assemblage composition and diversity were apparent with severe flow reduction, for assemblages of riffles, runs and pools:

- Increased invertebrate densities were found within riffle patches, due to packing of obligate rheophiles and a number of other common rheophilic taxa into reduced wetted area (e.g. Simuliidae, Hydroptilidae). While plausibly, certain species might have been favoured by local conditions and proliferated through

rapid generation turnover there was less evidence to support this response. Either way, increased crowding of individuals led to early signs of biotic interactions that might have played an increasingly greater role in local species persistence had low flow conditions been protracted.

- Emigration of taxa occurred from riffles into less stressful microhabitats within-patch, where these existed, including deeper into the underlying substratum, or into adjoining patches still connected by flowing surface water, that acted as temporary flow refuges. Even obligate rheophiles relocated with the exceptional fragmentation and loss of riffle patches at severe low flows. The influx of taxa from the surrounding landscape into riffles was uncommon.
- Commonly, taxa relocated to the larger remaining run patches, some of which had hydraulically transformed to increasingly resemble riffles at extreme low flows (e.g. Chironomidae, elmid larvae, acarinids, Empididae, Baetidae), with concomitant gains in taxa or individuals in run patches and increased overlap of riffle and run assemblage composition.
- Certain pools quite often lost taxa and individuals with discharge reduction. In other instances, pools gained invertebrates at very low flows with loss of wetted area, usually from runs or less commonly, and only in extreme cases, from riffles. The latter effect was not observed for entire assemblages with lesser discharge reduction or at natural low flows (when the limited taxonomic overlap of riffle and pool assemblages reflected hydraulic extremes). Certain of the more mobile riffle taxa showed sufficient breadth in hydraulic tolerances to be able to utilise pool refuges, at least in the short-term (e.g. Elmidae larvae).
- Shifts in stone microdistribution patterns from those established at natural low flows comprised a fundamental element of the invertebrate redistribution dynamics observed at hydraulic biotope scale, reinforcing the observed redistribution mechanisms within the broader biotope mosaic.

Diversity and low flows

Almost all diversity indices showed increases, though seldom statistically significant, as natural flows dropped to their lowest levels midsummer, across river reaches and for all biotopes. However, artificial discharge reduction to extremely low levels led to converse responses in diversity from natural in more than 70% of cases examined. Where changes in invertebrate diversity in relation to abnormal flow reduction were inconsistent, it commonly reflected different directions of response among biotopes with faunal redistribution. This finding supported the need to examine responses by hydraulic biotope (mesohabitat) type and with explicit recognition of landscape patchiness in flow impact.

- Total number of taxa (and taxon richness) was perhaps the most consistent measure of invertebrate response to low flow disturbance of all diversity indices. However, while extreme flows reduced the mean numbers of families below those of un-impacted assemblages during the lowest flow months across biotope types, most notably for riffles, and for all flow-disturbed rivers, declines were neither significant nor proportional to flow diversion magnitude.

- Least consistency in responses was apparent across the flow-disturbed rivers and biotopes when diversity was expressed in terms of the numbers of individuals, assemblage evenness or Shannon-Weiner diversity. Both extremely high and very low abundances were encountered at lowest flows, suggesting that increased faunal variability might be a prominent feature of low-flow disturbance generally and merit attention as an ecologically useful measure in and of itself.

Shifts in invertebrate biotope specificity and hydraulic preferences at low flows

While trajectories or abrupt thresholds of invertebrate response (Boulton 2003) were less obvious than abiotic thresholds of change in response to extreme flow reduction (e.g. flushing of accumulated poor water quality; biotope patch transitions and isolation), they clearly centered on the progressive loss of biotope specificity and breakdown of invertebrate associations with microhabitat hydraulics, as well as reversals in trend directions (e.g. for diversity) from those at natural low flows. Across all flow disturbed reaches, although the hydraulic integrity of individual biotopes intensified with extreme flow reduction their biological integrity weakened, with variable decoupling of patch character and invertebrate hydraulic preferences, a tendency already evident at naturally lowest flows.

- At natural dry-season flows, some 58% of all common invertebrate families recorded showed distinct affinities for particular biotope types, with the remainder appearing to be flow-hydraulics generalists.
- Under conditions of artificially reduced flows, this proportion had decreased dramatically. Some two-thirds of the same families no longer showed detectable among-biotope preferences, and the strengths of association with different biotopes for those taxa still showing some biotope specificity had also declined.

The loss of detectable biotope specificity for individual taxa was corroborated by evidence of losses in the strength of their various relationships with the hydraulics of habitat, with the shift from natural to altered low flows.

- At natural low flows, invertebrates showed numerous consistent and significantly strong associations (based on densities), many of which held across multiple rivers, with one or more of the principal hydraulic factors used to characterize biotopes and microhabitats. Different taxa exhibited specific tolerance ranges and thus, different responses, to this suite of hydraulic attributes, with a core group of some 17 taxa highly responsive to almost all of them (e.g. Hydropsychidae, *Rheotanytarsus fuscus*).
- With severe flow reduction, the majority of taxa lost all or most of their significant associations with hydraulic factors (e.g. Hydropsychidae, Hydroptilidae and Athericidae). Very few taxa (e.g. Simuliidae and Chironomidae, including three riffle-associated chironomid species) retained all of their previously significant hydraulic relationships once flows became severely reduced. For these taxa and certain others (e.g. Baetidae, Acarina), select hydraulics-density relationships were strengthened during altered flows.
- It was evident from the varying extents to which different invertebrate taxa, including those known to show significant biotope specificity, remained linked to hydraulic conditions, that there were two basic

responses to hydraulic changes with low-flow disturbance. These taxon-specific shifts with flow disturbance were verified for indicator taxa, using habitat suitability index curves:

- In the majority of cases, many of the invertebrate taxa appeared either to possess significant breadth of hydraulic tolerance or to be able to adapt, at least in the short-term, so as to endure hydraulically marginal conditions, whether by remaining in the same patch or having to relocate to another. Few taxa appeared to be living in their preferred microhabitats under very low flows.
- Less commonly, certain taxa (e.g. Simuliidae, Baetidae, Chironomidae and Elmidae) demonstrated an intensified effort by individuals to remain or concentrate in areas of optimal hydraulic conditions (where still feasible based on local patch and broader landscape conditions).

- It might be simplistic, therefore, in many instances, to consider invertebrates as flow or hydraulics specialists at very low flows, with a significant complement of the benthos exhibiting a highly developed ability, behavioural or otherwise, to adapt to low flow dynamics. While flow sensitive taxa could be identified at hydraulic microhabitat and biotope scales, as well as with regards direct responses to discharge, the observed dissolution of preferences for most taxa introduced a new dimension to the selection and use of flow indicators.

9.1.6 Ecologically relevant low flows for invertebrates

Characterization of ecologically relevant low flows over immediate, as well as monthly, flow timeframes was most effective when indices of biological response were explicitly linked with not only indices reflecting differences in site low-flow histories, but also abiotic measures reflecting more immediate changes in habitat conditions. (At an annual scale, environmental factors other than flow were not addressed.) Invertebrates responded most strongly to an integrated suite of indices, namely:

1. A subset of those flow indices identified as potentially ecologically relevant.
2. Physical habitat represented using (i) key discharge-responsive hydraulic attributes, and (ii) biotope-specific patch metrics.
3. Select chemical parameters - though the specific factors were highly variable in each instance, inclusion even of slight secondary changes in water quality at low flows considerably strengthened overall relationships between invertebrate composition and abiotic state.

Measures of immediate flow conditions and invertebrate response

The ‘immediate flow’ window encompassing the flow-disturbance timeframe of days to weeks (within a single season, over the sampling period) clearly bridged scales of hydraulic to hydrologic influence. While instantaneous discharge magnitudes overall significantly and directly affected trends in mean densities of a substantive 19 invertebrate families, across multiple rivers and biotopes, few responses were consistent in direction or strong - generalised relationships were only possible for two taxa. On their own, diversity measures for riffle assemblages (the biotope type examined in greater depth) also tended not to be useful

mirrors of direct invertebrate response to instantaneous discharge, though where apparent, diversity trends reinforced the observed flow-mediated patch redistributions. Trend directions clearly depended on: taxon biotope and hydraulic preferences, and the extent to which those could be adjusted at unnaturally low discharges; disturbance intensity (magnitude and areal patchiness); and degree of local deterioration in patch conditions. Discharge-related changes in key hydraulic factors (e.g. Fr, VD_{ratio}, NBV, 0.6V, and at severe low flows, RE), biotope-specific patch metrics that reflected the availability of preferred habitat (riffle wetted surface area, width and perimeter), and commonly, electrical conductivity, exerted greater influences on riffle assemblage composition than instantaneous flow magnitudes alone.

Monthly indices of potential flow disturbance

Only monthly flow variability (CV) did not appear an ecologically relevant variable for any of the 32 most common summer invertebrates, but 15 other potentially ecologically relevant monthly flow indices were significantly influential. There were numerous (73) positive and negative relationships with densities of 22 invertebrate families at natural low flows, more so than for annual flow indices, though across a similar total number of families. In isolation of other types of variables, the most biologically influential flow index within this temporal window was actually instantaneous discharge, but expressed as a monthly percentile, closely followed by monthly median Q_{7dLow} and monthly Q_{max} (effectively encompassing the range of low to high flows). Monthly minimum (Q_{min}) and median (Q_{50}) flows were also detectably linked to invertebrate response. Certain families exhibited higher densities at low values of monthly indices such as Q_{min}, median Q_{7dLow} and Q_{50}, and might therefore possess enhanced tolerances for naturally lower flows (e.g. Elmidae, Leptoceridae, Notonemouridae, Hydroptilidae and Oligochaeta). Other taxa showed the converse pattern (e.g. Heptageniidae and two other ephemeropteran families, hydropsychids, Philopotamidae and Limnichidae).

As with the 'immediate flow' disturbance timeframe, monthly flow indices assumed lesser importance than metrics of reach abiotic conditions at the actual time of flow disturbance, in structuring invertebrate assemblages at low flows. The most useful variables overall were:

- A cohesive group of descriptors of available physical habitat (i.e. total wetted surface area and width), its degree of streambed connectivity, and whether or not it provided flowing-water conditions (e.g. velocity ≤ 0.01 m s^{-1}, and NBV or Fr).
- A more diverse set of chemical variables that generally included EC and nutrients.
- A consistent series of monthly flow indices, principally Q_{95} and monthly Q_{max}. The percentile, Q_{95}, was more prominent at this time step than at the finer temporal scale, while interestingly, median Q_{7dLow} and instantaneous flows were of limited influence once other abiotic factors were included.

Annual flow indices and invertebrate response

Twenty of the 32 most common invertebrate taxa across the sites were responsive, in densities, to a total of 21 different annual measures of natural flow-disturbance history (e.g. Caenidae, Hydraenidae and two odonate families) with various influential trends (41) identified between flow variables and individual families. Several of the taxa differed from those more strongly associated with monthly flow indices. A few of the annual flow indices bore little influence on the mean abundances of any dominant taxa at the sites: annual median Q_{7dLow}, Q_{50}, Q_{80}, and Q_{min} and its corresponding CV. A number of families, among them the Teloganodidae, Hydraenidae and Corydalidae, showed marked positive relationships with indices reflecting higher degrees of flow predictability, annually and during the peak months of the dry season. Concomitantly, they showed negative relationships with measures of flow variability, based on CV, for the same timeframes, and with indices reflecting high flows. Similarly caenids, for example, exhibited higher densities at higher values of most low flow percentiles, but were negatively linked with flood events and their year-to-year variability. Flow regime predictability (*P*), and constancy (*C*), as well as flow magnitude (annual low flow index, Q_{95}, combined with measures of average and high flows, e.g. annual average and median discharge, Q_5 and annual volume) were important disturbance attributes to which invertebrates responded, and matched well with natural dry-season assemblage composition. The low-flow variables, MAM, Q_{99}, Q_{90} and flow contingency were also fairly influential.

Relative ecological influence of various flow indices

It was evident that the hydrological regime had a defining role both in terms of the invertebrate responses elicited by different magnitude dry-season low flows, as well as the long-term flow disturbance history to which the biota was adapted. Even in the context of the low-flow period, high flow indices remained important in influencing summer assemblage composition and response to flow disturbance. Not all of the flow indices found most effective in representing river hydrological character could be usefully connected to invertebrate response, and hence, be considered truly ecologically relevant. Moreover, no single suite of flow indices consistently characterized low flows for invertebrate assemblages across rivers. Different responses by the same and by different invertebrate taxa (common to all rivers) also were found for measures of immediate flow conditions, monthly (including within dry season) flow indices, and long-term annual and inter-annual flow indices.

Rivers with varying flow regime characteristics might be expected to respond in quite different ways to the same low-flow disturbances, even within the same regime type, across a gradient of flow event variability and predictability. Low flow indices were unlikely to act adequately as ecologically meaningful surrogates for invertebrate low flow requirements when considered alone, particularly in cases of isolated, shorter-term unnatural disturbances. Results strongly suggested that short-term low-flow disturbance might be most effectively described at the hydraulics-hydrology interface, using a combination of biotope-scale hydraulic and patch habitat (physical and chemical) descriptors, key daily to monthly flow indices (representing low

flows, but not to the exclusion of select annual high flow metrics), and flow-related changes in water quality (even where such changes might be slight for anthropogenically least-impacted streams). Ecologically relevant flows for invertebrates under prolonged low-flow disturbance might be most effectively reflected by a wide suite of predominantly annual flow indices, comprising: influential monthly-scale flow indices, including low flow percentiles; indices of low-flow regime predictability and constancy (annual and seasonal); and a small set of high flow measures that include magnitude.

9.2 FUTURE RESEARCH DIRECTIONS

The following recommended areas of research are aimed at addressing just some of the many areas of uncertainty remaining in the characterization of ecologically meaningful low flow events, with particular emphasis on benthic macroinvertebrates. Presently, despite the varied studies mentioned throughout this thesis, research on the effects of low flow regimes on invertebrates remains insufficient to fully address the conservation and flow management challenges of perennial rivers.

Within ecohydrological science, effort needs to be invested in a framework for more structured low flow research in perennial rivers that guides areas such as:

- The disaggregation of the hydrological regime into disturbance-relevant temporal windows of low flow (i.e. instantaneous to daily, monthly, annual and inter-annual; building on, among others, Puckridge *et al*. 1998; Lake 2003).
- The selection of suites of low flow indices, validated scientifically as ecologically relevant, appropriate for these various time frames and associated with the key low-flow events.
- Approaches for linking individual flow-disturbance events to the historical flow record (many studies do not tie biotic response back to the natural disturbance regime), and for addressing gradients of variability in low-flow disturbance both within and across different river hydrological types.

Antecedent flow events are seldom explicitly factored into investigations of flow disturbance, yet have the potential to influence biotic responses to low-flow perturbations.

- How important is the role of recent antecedent events, and over different time periods, when compared to the long-term historical flow regime, in affecting invertebrate responses to low flows?
- Do fresh events during the dry season act as disturbance spikes that induce invertebrate response and reset elements of the stream system at a small scale, as similarly occurs with large-scale floods?

The magnitude of discharge reduction remains the primary focus of low-flow studies, with less effort invested in understanding other flow criteria such as frequency, timing, duration extents (outside of droughts), and rate of change (mostly addressed with hydropower or inter-basin water transfers). Further work is required to consolidate existing understanding and build a more substantive body of knowledge:

- In what ways, to what extent, and within which temporal and spatial scales do these different attributes of low flow events play varying and synergistic roles in effecting physical disturbance?
- What are the effects of seasonal flow reversals and augmented discharges during the dry season, as flow disturbances?

Thesis findings have suggested that short-term low-flow disturbance might be most effectively described by a combination of metrics of reach abiotic conditions at the time of disturbance and flow indices of an approximate monthly time step. Longer-term disturbances might more readily be characterized by relating annual flow indices directly to invertebrate responses based, for example, on life history traits. There remains considerable work to identify an appropriate, scale-based suite of multiple indicators of disturbance based on physical habitat, water chemistry and hydrological regime, and invertebrate response, to characterize low-flow disturbance for different perennial rivers. Such indicators would need to be as consistent and generalized as feasible across flow regime types and flow gradients within-types, and different hydrologic states (reduced flow, flow cessation, fragmentation, etc.). They would also need to consider the influences of multiple stressors (Whittington 2000; Suren *et al*. 2003; Dewson *et al*. 2007a), especially where sites are already subject to human impacts. Once established, such indicators might allow the development of profiles of invertebrate response to low flow events, for various categories of low-flow disturbance and different flow regime types (e.g. O'Keeffe *et al*. 2002; Poff *et al*. 2010).

Hydraulic biotopes are now established as both hydraulically and ecologically relevant patch units in relation to different flow regimes and river types, though further validation is needed of their longer-term hydraulic and ecological integrity, and of the relative contributions of low and high flow events to their maintenance. Evidence from this and other flow-physical habitat studies and their implications for invertebrate pathways of response to low-flow perturbations, underscores a growing need for more sophisticated, multi-dimensional modelling of biotope (mesohabitat) patch dynamics, from which ecohydraulics specifically stands to benefit.

- At high flows, probable locations of disturbed patches and intensity of disturbance can be predicted based on factors such as bed substratum movement. Similar predictive models of differential streambed disturbance over multiple low flow periods of differing lengths and geomorphic scales, based on criteria such as the likelihood of fragmentation or isolation of key habitat features (e.g. pools), might yield new insights into flow-invertebrate dynamics. Partitioning the disturbance event according to flow phases or different temporal windows might assist in such model development.
- Additional studies of the transition probabilities between different biotope patch types or patch sequences with low flows, reflected as specific low flow percentiles or other flow indices, as attempted in this thesis, might yield useful thresholds of potential flow stress for invertebrate fauna.
- Tremendous potential exists to explore relationships between various spatially explicit patch metrics (and across multiple patch types), low flows and biotic response, in the landscape mosaic, as well as to elucidate the primary redistribution pathways of invertebrates.

- Evidence from this and other studies has suggested that a simpler patch habitat architecture and landscape mosaic might result in reduced hydraulic habitat diversity, fewer flow refuges and hence, by implication, greater potential for more intense impacts of extremely low flows on the benthos. This topic merits focused investigation and might have particular implications for anthropogenically modified rivers, many of which experience habitat simplification.

At larger river scales, flow-linked cues are well known to trigger biotic responses. What were the low flow-mediated cues at small habitat patch scales (e.g. subtle chemical changes, intensified biotic interactions) that activated redistribution responses for different invertebrate taxa?

- At extremely low flows, while biotopes retained their same type, their 'hydraulic composition' changed. Further work is needed to confirm whether or not such a change in patch hydraulics represented a catalyst for particular invertebrate responses, and as such could be utilised as a threshold in ecohydrological monitoring.
- What prompts invertebrates to recognize that discharges are changing? When do they elect to relocate (and by which mechanism) or to remain, and in some cases modify their behaviour, to tolerate the changed conditions?
- For what lengths of time are benthic macroinvertebrates able to cope with the sub-optimal hydraulic conditions and other stresses generated by extreme low flows? Many taxa are already in highly marginal habitat conditions and likely approaching limits of tolerance. This is particularly true of the transition from very low flows to substratum exposure, where more is presently known about the degrees of tolerances to dewatering of temporary than perennial lotic invertebrates.

Perennial pool biotas are often subjected to a highly localised, diverse set of environmental changes with extreme flow reduction.

- What are the relationships between pool assemblage composition and pool physical state at both natural and unnatural low flows? Research on effects of natural low flows appears rather scarce.
- Why are certain isolated biotopes more physically, chemically and biologically altered by flow reduction than others - what are the main contributing factors?
- What are the species traits of pool taxa that allow them to tolerate the wider diversity of pool conditions in perennial systems and how many are in common with invertebrates of temporary pools?
- Is there a shift in flow disturbance towards pools becoming more disturbed than riffles at high flows, as suggested by some authors – might this influence the species traits of the more habitual pool dwellers?

Limited effort has been focused on the relative low flow sensitivity of invertebrate taxa, with most research thus far having looked simply at velocity and/or general flow features as approximations of flow sensitivity. The development of new indices based on the flow sensitivity (degree of responsiveness) of invertebrate taxa, or the development of long-term flow preference relationships for individual taxa for specific flow events and associated flow criteria, could contribute to detection and measurement of the impacts of

hydrologic alteration. It might then also be possible to establish more rigorous flow sensitivity indices for rapid bioassessment of flow alteration or routine monitoring of implemented environmental flows. There is now sufficient information accumulated to at least more accurately identify flow sensitive and generalist taxa across different biophysical settings and river regime types.

In this study, various invertebrate taxa responded to groups of flow indices representing different time scales in flow history and flow event characteristics. What indications do the combinations of monthly and annual flow indices with which individual invertebrate taxa are most strongly associated provide as to the attributes of their life history strategies related to flow disturbance? While efforts are underway to consolidate understanding of the modes of adaptation of riverine biota to flow events, there is a great deal that remains to be learnt about the nature of invertebrate responses to the abiotic changes, as well as the biotic interactions among individuals and species, during episodes of flow-related stress such as are liable to occur at extreme low flows.

9.3 CONCLUSIONS: APPLICATION IN ENVIRONMENTAL FLOW SCIENCE FOR RIVER MANAGEMENT

9.3.1 Application in environmental flow science and practice

As a comparatively new, rapidly evolving area of freshwater science, ecohydrology has provided fertile grounds for not only applied research but also the revitalisation of stream ecosystem theory, including that addressing disturbance. As Collins and Glenn (1997) observed, the increasing emphasis given to mimicking natural disturbance regimes in human managed systems relies on a sound understanding of the effects of disturbance on ecosystem processes and biota. While there are growing efforts to validate the collective body of theory that constitutes the conceptual framework of ecohydrology (e.g. Boulton 2003; Lake 2003; Hannah *et al*. 2004; Lytle and Poff 2004; Arthington *et al.* 2006; Death *et al*. 2009; Poff *et al*. 2010), efforts to provide flow-ecology knowledge in a form useable in river flow management need to be intensified.

Environmental flow science has generated a demand for understanding of ecological responses to hydrologic change within and among rivers, and yet is still strongly governed by expert judgement and assumptions that have yet to be empirically grounded. To this end, river ecologists ought to embrace transdisciplinarity, to become practicing ecohydrologists who not only appreciate the functional connections among the disciplines of hydrology, geomorphology and ecology, but adopt elements of these areas of science within their research (Gustard and Bullock 1991; Jewitt *et al*. 2001; Hannah *et al*. 2004). They also need to become more adept at effectively conveying the knowledge gained to society, for its full uptake and use in river conservation and management (Dunbar and Acreman 2001; Naiman *et al.* 2006; Rogers 2006).

With the growing attention accorded hydrology-ecology interrelationships and the ecological characterization of river flow regimes, encouragingly a hierarchical view of river ecosystems in relation to

flow variability and geomorphic spatiotemporal scales is increasingly being adopted. The work conducted in this thesis, where flow reduction was found to be most ecologically meaningful, from the perspective of benthic macroinvertebrates, when placed in the context of the natural hydrological regime and at specific habitat scales, lent firm support for this direction. Such low-flow disturbance studies are revealing the profound influence of both individual hydrological events and the long-term flow disturbance history on invertebrates, particularly as multi-river comparisons of flow regimes and their biotic implications continue to rise (e.g. Castella *et al.* 1995; Death and Winterbourn 1995; Poff 1996; Clausen and Biggs 1997; Riseng *et al.* 2004; Monk *et al*. 2006, 2007; Konrad *et al*. 2008). Ecologically relevant flow indices are gaining prominence in this regard, including within environmental flow science. Future attention needs to be directed at what constitutes actual ecological meaning in relation to different hydrograph elements and timeframes. As found in this study, screening of potentially ecologically relevant flow indices prior to their application, by examining their interrelationships with various descriptors of ecosystem response, is vital.

Similarly, placing invertebrate response to flow disturbance within an established geomorphological hierarchy, as is more regularly attempted, accentuates the critically influential role of the habitat template at landscape and patch scales, and vastly improves the scope for generalizations of flow-ecology responses within and among rivers. In this regard, ecohydraulics specifically appears set to remain a core and active research field embedded within ecohydrology, and a central aspect of environmental flow approaches for years to come. As demonstrated in this thesis, and building on earlier research, hydraulic habitat is a key intermediary in the connection between low flow and ecological response for instream biota. The biotope, particularly, was shown to be a hydraulically and ecologically relevant patch unit that has the potential to bring together and integrate current mesohabitat and microhabitat approaches to low flow assessment. With the inclusion of specific elements and metrics borrowed from landscape ecology and patch dynamics, flow-biotope analyses represent one of the more promising and yet under-investigated avenues for establishing flow-invertebrate response relationships. Measures of the breakdown of invertebrate assemblage and taxon biotope and hydraulic habitat preferences, shown in this thesis at patch mosaic, individual biotope and microhabitat scales, for example, would seem to be one suitable suite to incorporate in such relationships, for determining and monitoring environmental flows.

While fundamentally an appropriate approach, hydrology-ecology modelling needs to shift from either focusing exclusively on hydraulic (meso)habitat or direct biological response to specific flow events, to more routinely melding the two approaches when dealing with invertebrate responses to flow alteration. Surprisingly, physical or chemical habitat conditions also are seldom quantified alongside invertebrate response to flow change, or the converse, despite the distinct bearing abiotic condition has on the nature of faunal response. As Riseng *et al.* (2004) emphasised, an understanding of the response of lotic communities to combinations and gradients of physical disturbance is central to the practical flow management of riverine ecosystems. Even within the biophysically similar perennial rivers of this study, there was a detectable

gradient of invertebrate response to low-flow disturbance founded on historical flow variability, and short-term flow state coupled with secondary disturbance effects on hydraulic habitat.

Much of the study of flow disturbance over the past decades has focused on perennial versus temporary systems, or on studies of individual rivers, rather than flow gradients *per se* or the disaggregation of flow history into ecologically meaningful temporal units. It may prove insightful in future studies of flow disturbance to examine abiotic and faunal responses along a gradient of flow variability, as an organising factor (e.g. Feminella 1996), rather than solely segregating response models based on a river's flow type. For either approach to be more effective for predictive purposes, however, there needs to be a greater effort expended to assess changes in biophysical conditions during natural, non-extreme periods of low flow. Part of the difficulty in ascribing changes in biophysical conditions in perennial rivers at low flows to specific stress factors stems from the dearth of information on the natural (reference) state and expected responses of rivers during low flows. Without such understanding, it remains difficult to meaningfully connect near-term responses to flow history, or to make explicit ecological risk.

The findings of this study suggest also that the extensive natural variability shown by the biota in response to low flow alteration is an important element of that response and, as such, should be factored into ecohydrological analyses. Research is now underway (e.g. Konrad *et al*. 2008) that highlights the benefits to be gained by investigating the kinds of invertebrate response to low flows isolated in this study using not only measures of central tendency and central response models, but also models based on limiting responses described by ceilings and floors. In doing so, the scatter and thus, potential contributing roles of multiple factors in constraining response would be particularly acknowledged (Palmer *et al.* 1997; Lancaster and Belyea 2006). A mix of relationships of varying strength and consistency were found in this study between flow disturbance indices and invertebrate response measures, though quite often of the same trend across variables or rivers. Consequently, a combination of models addressing both the central tendency of any response and, debatably possibly more importantly, its limits, would seem ideally suited to further attempts to distill out and characterize those low flow change-invertebrate response relationships that are most generic at various spatiotemporal scales, and thus, amenable for use in flow management.

9.3.2 Conclusions for river flow management

To ensure that ecohydrology continues its vital role in supporting effective river management, effort needs to be directed at expanding knowledge of the relationships between the flow characteristics of a river, its geomorphological setting and ecological condition (Englund and Malmqvist 1996; Richter *et al.* 1996; Hughes and Hannart 2003; Biggs *et al*. 2005; Poff *et al*. 1997, 2006). A full understanding of the natural hydrological history of a river is an indispensable aide in this regard, for assessing the biophysical implications of flow change. The results of this thesis support the need for the natural flow paradigm to become a more pervasive element of river ecological theory and environmental flow research. They add to the gradually mounting body of evidence that the natural flow regime of rivers exerts a profound influence

on aquatic biota, and that changes in flow patterns represent physical disturbances, the response pathways to which are complexly interwoven over varied spatiotemporal scales.

In general, different regimes of flow variability tend to support different ecological assemblages and associated life history strategies (e.g. Poff and Ward 1989; Poff *et al*. 1997; Biggs *et al*. 2005). The aquatic biota is not necessarily uniquely adapted to all attributes of an individual river's flow regime though, suggesting that some generalization of biotic responses to flow regime dynamics should be possible (Lytle and Poff 2004). An ability to characterize ecologically relevant flows for the biota is central to the development of recommendations for river flow management (Hooper and Ottey 1982; Monk *et al*. 2006). Bunn and Arthington (2002, p. 492) concluded, however, that although there is growing recognition of the ecological importance of specific elements of the flow regime, "ecologists still struggle to predict and quantify biotic responses to altered flow regimes". Moreover, there remain many unknowns related to the structural and functional aspects of interrelationships among flow, habitat and aquatic biota (Naiman *et al*. 2002; Death *et al*. 2009).

Certainly, the results of the present study illustrated some of the complexities inherent in deriving low flow-ecological response models for invertebrates particularly suited to generalisation across multiple rivers of the same hydrological type, for management purposes. There is clearly a balance to be sought between individual river signatures (with the full range of scientifically rewarding complexity they encompass) and the generality required for establishing flow rules for river management, as underscored by the results of this and other ecohydrological studies. Ward (1976, p. 248) commented many years previously that while generalizations are possible, numerous factors need to be considered when making them for regulated rivers in relation to their flow-related responses and the definition of appropriate flow criteria, such that "ultimately each river, indeed even different sections of the same river, must be considered individually". Currently ecohydrological science, while recognising and attempting to strike this balance, is limited by the number and depth of studies that move beyond simply documenting flow alteration and the responses it elicits, to isolating flow events and characterizing ecological response in a scale-dependent way that links explicitly to the flow disturbance regimes of different kinds of rivers.

There is obviously a need for the cross-exchange of information between river site-specific and more generic river type flow-ecology relationships in environmental flow practice. The Ecological limits of Hydrologic Alteration (ELOHA; Poff *et al*. 2010) represents one emerging regional framework for broad-scale environmental flow setting that holds considerable promise in this arena. It takes into consideration river-specific ecohydrological information in a structured way in its attempt to generalise across rivers of similar type within and beyond individual river basins. It therefore also effectively consolidates the currently largely scattered volume of evidence on flow alteration and ecological response to promote more informed river management. Ultimately, however, as the results of this study highlighted, it is important to consider the river as an individual response unit, at least while ecohydrology is in its infancy. Moreover, the study lends

support to the call for large-scale flow experiments to be conducted on individual rivers, with monitoring and adaptive refinement of recommended flow regimes (Poff and Ward 1989; Dunbar and Acreman 2001; Bunn and Arthington 2002; Arthington and Pusey 2003; Poff *et al*. 2003; Richter *et al.* 2006), as well as for supporting hydroecological research (Arthington *et al*. 1996).

Richter *et al.* (1997a, 2003), Naiman *et al*. (2002), and other ecohydrologists, were echoed by Bunn and Arthington (2002, p. 502) when they stated "Our limited ability to predict and quantify the biotic response to flow regulation is a major constraint to achieving ecological sustainability". Bunn and Arthington (*op. cit*.) concluded that "Ecologists still have much to learn about the ecological significance of individual flow events and sequences of events, and descriptive science can take us only so far in unraveling these linkages. The advice from aquatic ecologists on environmental flows might be regarded at this point in time as a series of largely untested hypotheses about the flows that aquatic organisms need and how rivers function in relation to flow regime. To overcome these problems, aquatic science needs to move into a manipulative or experimental phase, either by restoring flows, or taking away flows, and measuring ecosystem response." The work reported on in this thesis represented one attempt, among a growing number within the ecohydrology research community, to do just that.

Arthington and Pusey (2003, p. 389) stated that ideally in future "environmental water requirements would be defined, and alternative water resource developments or restoration scenarios evaluated, by means of quantitative predictive models of the relationships between hydrology and the ecological processes governing biological diversity and ecosystem integrity." Considerable and rapid progress has been made in this direction, despite the caveats discussed above, with environmental flow practice benefiting directly from such advancements (Tharme 2003; Arthington *et al*. 2006). The reality, however, is that rivers will continue to be hydrologically altered to meet increasing freshwater demands or persist in degraded states as a result of existing flow regulation. It is critical, therefore, that ecohydrologists take up the challenge to intensify even further their efforts to characterize ecologically relevant flows for riverine ecosystems and their biota, to ensure more scientifically rigorous and management adaptive approaches to environmental flows in the future - for the sake of our rivers and humankind.

REFERENCES

Aadland, L.P. 1993. Stream habitat types: their fish assemblages and relationship to flow. *North American Journal of Fisheries Management* 13: 790-806.

Abell, R. 2002. Conservation biology for the biodiversity crisis: a freshwater follow-up. *Conservation Biology* 16: 1435-1437.

Abramovitz, J.N. 1995. Freshwater failures: the crises on five continents. *World Watch* 8: 27-35.

Acreman, M.C., Farquharson, F.A.K., McCartney, M.P., Sullivan, C., Campbell, K., Hodgson, N., Morton, J., Smith, D., Birley, M., Knott, D., Lazenby, J., Wingfield, R. and Barbier, E.B. 2000. Guidelines for artificial flood releases from reservoirs to restore and maintain downstream wetland ecosystems and their dependent livelihoods. Final Report to DFID and World Commission on Dams. Centre for Ecology and Hydrology, Wallingford, United Kingdom. 86 pp.

Acreman, M.C. and King, J.M. 2003. Defining water requirements. Chapter 2: pp 11-30. In Dyson, M., Bergkamp, G. and Scanlon, J. (eds). 2003. *Flow. The essentials of environmental flows.* IUCN, Gland, Switzerland and Cambridge, U.K. xiv + 118 pp.

Acreman, M.C. and Dunbar, M.J. 2004. Methods for defining environmental river flow requirements - a review. *Hydrology and Earth System Sciences* 8: 121-133.

Adams, J. 1991. The impact of stream-flow storage in farm dams on the Upper Klein Berg River catchment. Unpublished B.Sc. (Honours) Thesis. Department of Environmental and Geographical Science, University of Cape Town. 146 pp.

Agarwal, A., Delos Angeles, M.S., Bhatia, R., Chéret, I., Davila-Poblete, S., Falkenmark, M., Villarreal, F.G., Jønch-Clausen, T., Kadi, M.A., Kindler, J., Rees, J., Roberts, P., Rogers, P., Solanes, M. and Wright, A. 2000. Integrated Water Resources Management. *TAC background papers No.* 4. Global Water Partnership, Technical Advisory Committee (TAC), GWP Secretariat, Stockholm, Sweden. 67 pp.

Agnew, C.T., Clifford, N.J. and Haylett, S. 2000. Identifying and alleviating low flows in regulated rivers: the case of the Rivers Bulbourne and Gade, Hertfordshire, U.K. *Regulated Rivers: Research & Management.* 16: 245-266.

Alexander, W.J.R. 1985. Hydrology of low altitude southern hemisphere landmasses. *Hydrobiologia* 125: 75-83.

Alfredsen, K. 1998. Habitat modelling in Norway - an overview of projects and future developments. pp. 33-35. In: Blažková, Š., Stalnaker, C. and Novický, O. (eds). 1998. *Hydroecological modelling. Research, practice, legislation and decision-making.* Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Alfredsen, K., Harby, A., Bakken, T.H. and Marchand, W. 1997. Application and comparison of computer models for quantifying impacts of river regulations on fish habitat. In: Broch, E., Lysne, D.K., Flatabo, N. and Helland-Hansen, E. (eds). *Proceedings from Hydropower 97.* Trondheim. June 29-July 1, 1997. Balkema.

Allan, J.D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics 35: 257-84.*

Allan, J.D. and Flecker, A.S. 1993. Biodiversity conservation in running waters. *BioScience* 43(1): 32-43.

Allanson, B.R., Hart, R.C., O'Keeffe, J.H. and Robarts, R.D. 1990. Inland waters of Southern Africa: an ecological perspective. *Monographiae Biologicae* 64. Kluwer Academic Publishers, Dordrecht. 458 pp.

Alstad, D.N. 1982. Current speed and filtration rate link caddisfly phylogeny and distributional patterns on a stream gradient. *Science* 216: 533-534.

Alves, M.H. and Henriques, A.G. 1994. Instream flow determination for mitigating environmental impact on fluvial systems downstream dam and reservoirs. Pp 351-358. In: Tsakiris, G. and Santos, M.A. (eds). *Advances in water resources and management*. A.A. Balkema, Rotterdam.

Alves, M.H., Bernardo, J.M. and Henriques, A.G. 1996. An approach for instream flow determination in Mediterranean rivers. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds). Ecohydraulics 2000. *Proceedings of the 2nd International Symposium on Habitat Hydraulics.* Québec, June 1996. INRS-Eau, Québec City, Canada. 9 pp.

Anderson, N.H. and Lehmkuhl, D.M. 1968. Catastrophic drift of insects in a woodland stream. *Ecology* 49: 198-206.

Anderson, P.W. and McCall, J.E. 1968. Effect of drought on stream quality in New Jersey. *American Society Civil Engineers Proceedings Paper 6138: Journal of Sanitary Engineering Division 94(SA 5)*: 779-788.

Annear, C.T. and Conder, A.L. 1984. Relative bias of several fisheries instream flow methods. *North American Journal of Fisheries Management* 4: 531-539.

Annear, T., Chisholm, I, Beecher, H., Locke, A., Aarrestad, P., Coomer, C., Estes, C., Hunt, J., Jacobsen, R., Jöbsis, G., Kauffman, J., Marshall, J., Mayes, K., Smith, G., Wentworth, R. and Stalnaker, C. 2004. *Instream flows for riverine resource stewardship*. *Revised edition*. Instream Flow Council, Cheyenne, Wyoming, U.S.A. 268 pp.

Armitage, P.D. 1977. Invertebrate drift in the regulated River Tees, and an unregulated tributary Maize Beck, below Cow Green dam. *Freshwater Biology* 7: 167-183.

Armitage, P.D. 1978. Downstream changes in the composition, numbers and biomass of bottom fauna in the Tees below Cow Green reservoir and in an unregulated tributary Maize Beck, in the first five years after impoundment. *Hydrobiologia* 58: 145-156.

Armitage, P.D. 1984. Environmental changes induced by stream regulation and their effect on lotic macroinvertebrate communities. Chapter III: Invertebrates. Pp. 139-165. In: Lillehammer, A. and Saltveit, S.J. (eds). *Regulated rivers*. Universitetsforlaget As, Oslo, Norway. 540 pp.

Armitage, P.D. 1995. Faunal community change in response to flow manipulation. Pp 59-78. In: Harper, D.M. and Ferguson, A.J.D. (eds). *The ecological basis for river management*. John Wiley and Sons Ltd, Chichester, U.K.

Armitage, P.D. and Petts, G.E. 1992. Biotic score and prediction to assess the effects of water abstractions on river macroinvertebrates for conservation purposes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2: 1-17.

Armitage, P.D. and Pardo, I. 1995. Impact assessment of regulation at the reach level using macroinvertebrate information from mesohabitats. *Regulated Rivers: Research & Management* 10: 147-158.

Armitage, P.D., Pardo, I. and Brown, A. 1995. Temporal constancy of faunal assemblages in 'mesohabitats' - application to management? *Archiv für Hydrobiologie* 133(3): 367-387.

Armour, C.L. and Taylor, J.G. 1991. Evaluation of the instream flow incremental methodology by U.S. Fish and Wildlife Service field users. *Fisheries* 16(5): 36-43.

Arthington, A.H. 1998a. Comparative evaluation of environmental flow assessment techniques: review of holistic methodologies. *Land and Water Resources Research and Development Corporation Occasional Paper No*. 26/98. Canberra, Australia. 46 pp.

Arthington, A.H. 1998b. Brisbane River trial of a Flow Restoration Methodology (FLOWRESM). Pp 35-50. In: Arthington, A.R and Zalucki, J.M. (eds). *Water for the environment: recent approaches to assessing and providing environmental flows*. Proceedings of AWWA forum. AWWA, Brisbane, Australia.

Arthington, A.H., Bunn, S.E., Pusey, B.J., Blühdorn, D.R., King, J.M., Day, J.A., Tharme, R.E. and O'Keeffe, J.H. 1992. Development of an holistic approach for assessing environmental flow requirements of riverine ecosystems. In: Pigram, J.J. and Hooper, B.P. (eds). *Proceedings of an international seminar and workshop on water allocation for the environment*. November 1991. The Centre for Water Policy Research, University of New England. Armidale, Australia. 282 pp.

Arthington, A.H. and Pusey, B.J. 1993. In-stream flow management in Australia: methods, deficiencies and future directions. *Australian Biology* 6: 52-60.

Arthington, A.H. and Lloyd, R. (eds). 1998. Logan River trial of the Building Block Methodology for assessing environmental flow requirements. *Published Workshop Report*. Centre for Catchment and In-stream Research and Department Natural Resources, Brisbane, Australia. 85 pp.

Arthington, A.H. and Zalucki, J.M. (eds). 1998a. Comparative evaluation of environmental flow assessment techniques: review of methods. *Land and Water Resources Research and Development Corporation Occasional Paper No*. 27/98. Canberra, Australia. 141 pp.

Arthington, A.H. and Zalucki, J.M. (eds). 1998b. Water for the environment: recent approaches to assessing and providing environmental flows. *Proceedings of AWWA Forum, Canberra, Australia*. AWWA, Brisbane, Australia. 144 pp.

Arthington, A.H., Brizga, S.O. and Kennard, M.J. 1998a. Comparative evaluation of environmental flow assessment techniques: best practice framework. *Land and Water Resources Research and Development Corporation Occasional Paper No.* 25/98. Canberra, Australia. 26 pp.

Arthington, A.H., Pusey, B.J., Brizga, S.O., McCosker, R.O., Bunn, S.E. and Growns, I.O. 1998b. Comparative evaluation of environmental flow assessment techniques: R and D requirements. *Land and Water Resources Research and Development Corporation Occasional Paper No.* 24/98. Canberra, Australia. 26 pp.

Arthington, A.H., Brizga, S.O., Choy, S.C., Kennard, M.J., Mackay, S.J., McCosker, R.O., Ruffini, J.L. and Zalucki, J.M. 2000. *Environmental flow requirements of the Brisbane River downstream of Wivenhoe Dam*. South East Queensland Water Corporation, Brisbane, and Centre for Catchment and In-Stream Research, Griffith University, Brisbane, Australia. 539 pp.

Arthington, A.H. and. Pusey, B.J. 2003. Flow restoration and protection in Australian rivers. *River Research and Applications* 19 (5-6): 377-395.

Arthington, A.H, Tharme, R.E., Brizga, S.O., Pusey, B.J. and Kennard, M.J. 2004. Environmental flow assessment with emphasis on holistic methodologies. Volume II: Pp 37-66. In: Welcomme, R. and Petr, T. (eds). *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries: sustaining livelihoods and biodiversity in the new millennium.* 11-14 February 2003. Phnom Penh, Cambodia. RAP publication 2004/17. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand.

Arthington, A.H., Bunn, S.E., Poff, N.L. and Naiman, R.J. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications* 16(4): 1311-1318.

Bain, M.B., Finn, J.T. and Booke, H.E. 1988. Streamflow regulation and fish community structure. *Ecology* 69: 382-392.

Barmuta, L.A. 1989. Habitat patchiness and macrobenthic community structure in an upland stream in temperate Victoria, Australia. *Freshwater Biology* 21: 223-236.

Baron, J.S., Poff, L.N., Angermeier, P.L., Dahm, C.N., Gleick, P.H., Hairston, Jr., N.G., Jackson, R.B., Johnston, C.A., Richter, B.D. and Steinman, A.D. 2002. Meeting ecological and societal needs for freshwater. *Ecological Applications* 12(5): 1247-1260.

Beisal, J.N., Usseglio-Polatera, P., Thomas, S. and Moreteau, J.C. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* 389: 73-88.

Bender, E.A. and Case, T.J. and Gilpin, M.E. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65(1): 1-13.

Benetti, A.D., Lanna, A.E. and Cobalchini, M.S. 2002. Current practices for establishing environmental flows in Brazil. Unpublished paper. *Environmental Flows for River Systems Working Conference and Fourth International Ecohydraulics Symposium*. 3-8 March 2002, Cape Town, South Africa.

Beran, M.A. and Gustard, A. 1977. A study into the low-flow characteristics of British rivers. *Journal of Hydrology* 35: 147-157.

Bergkamp, G., McCartney, M., Dugan, P., McNeely, J. and Acreman, M.C. 2000. Dams, ecosystem functions and environmental restoration. *WCD Thematic Review - Environmental Issues* II.1. World Commission on Dams. Secretariat of the World Commission on Dams, Cape Town, South Africa. 187 pp.

Bernstein, B.B. and Zalinski, J. 1983. An optimum sampling design and power tests for environmental biologists. *Journal of Environmental Management* 16: 335-343.

Bickerton, M.A. 1995. Long-term changes of macroinvertebrate communities in relation to flow variations: the River Glen, Lincolnshire, England. *Regulated Rivers: Research & Management* 10: 81-92.

Bickerton, M., Petts, G., Armitage, P. and Castella, E. 1993. Assessing the ecological effects of groundwater abstraction on chalk streams: three examples from eastern England. *Regulated Rivers: Research & Management* 8: 121-134.

Biggs, J.F. and Close, M.E. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology* 22: 209-231.

Biggs, B.J.F., Duncan, M.J., Jowett, I.G., Quinn, J.M., Hickey, C.W., Davies-Colley, R.J. and Close, M.E. 1990. Ecological characterisation, classification and modelling of New Zealand rivers: an introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research* 24: 277-304.

Biggs, B.J.F., Duncan, M.J., Francoeur, S.N. and Meyer, W.D. 1997. Physical characterisation of microform bed cluster refugia in 12 headwater streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 413-422.

Biggs, B.J.F., Nikora, V.I. and Snelder, T.H. 2005. Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications* 21: 283-298.

Birkhead, A.L., Van Coller, A.L., James, C.S. and Heritage, G.L. 1996. Modelling water availability to riparian vegetation in an impacted river system. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds*). Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics.* Québec, June 1996. Volume B. INRS-Eau, Québec.

Birkhead, A.L. and James, C.S. 1998. Synthesis of rating curves from local stage and remote discharge monitoring using nonlinear muskingum routing. *Journal of Hydrology* 205: 52-65.

Black, A.R., Bragg, O.M., Duck, R.W. and Rowan, J.S. 2002. Development of a method to assess ecological impact due to hydrological regime alteration of Scottish rivers. Pp. 45-51. In: The structure, function and management implications of fluvial sedimentary systems. Proceedings of an international symposium held at Alice Springs, Australia, September 2002. *IAHS Publ. No.* 276. Alice Springs, Australia.

Blažková, Š., Stalnaker, C. and Novický, O. (eds). 1998. *Hydroecological modelling. Research, practice, legislation and decision-making*. Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Bond, P. and Goldblatt, P. 1984. Plants of the Cape flora. A descriptive catalogue. *Journal of South African Botany Supplementary Volume* 13: 1-455.

Boon, P.J., Calow, P. and Petts, G.E. (eds). 1992. *River conservation and management*. John Wiley and Sons, Chichester, U.K.

Boon, P.J., Davies, B.R. and Petts, G.E. (eds). 2000. *Global perspectives on river conservation: science, policy and practice*. John Wiley and Sons, Chichester, U.K. 517 pp.

Bottorff, R.L. and Knight, A.W. 1988. Functional organization of macroinvertebrate communities in two first-order California streams: comparison of perennial and intermittent flow conditions. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1147-1152

Bouckaert, F.W. and Davis, J. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology* 40: 77-86.

Boulton, A.J. 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of South Australia* 113: 23-34.

Boulton, A.J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology* 48: 1173-1185.

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams - an Australian perspective. Pp. 313-327. In: De Deckker, P. and Williams, W.D. (eds). *Limnology in Australia*. CSIRO/Dr W. Junk Publishers, Melbourne and Dordrecht.

Boulton, A.J. and Lake, P.S. 1988. Australian temporary streams - some ecological characteristics. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1380-1383.

Boulton, A.J., Spangaro, G.M. and Lake, P.S. 1988. Macroinvertebrate distribution and recolonization on stones subject to varying degrees of disturbance: an experimental approach. *Archiv für Hydrobiologie* 113(4): 551-576.

Boulton, A.J. and Lake, P.S. 1990. The ecology of two intermittent streams in Victoria, Australia. I: Multivariate analyses of physicochemical features. *Freshwater Biology* 24: 123-141.

Boulton, A.J. and Lake, P.S. 1992a. The ecology of two intermittent streams in Victoria, Australia. II: Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology* 27: 99-121.

Boulton, A.J. and Lake, P.S. 1992b. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology* 27: 123-138.

Boulton, A.J., Peterson, C.G., Grimm, N.B. and Fisher, S.G. 1992a. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73(6): 2192-2207.

Boulton, A.J., Stanley, E.H., Fisher, S.G. and Lake, P.S. 1992b. Over-summering strategies of macroinvertebrates in intermittent streams in Australia and Arizona. Pp. 227-237. In: Robarts, R.D. and Bothwell, M.L. (eds). Aquatic ecosystems in semi-arid regions: implications for resource management. *N.H.R.I. Symposium Series* 7. Environment Canada, Saskatoon, Canada.

Boulton, A.J., Valett, H.M. and Fisher, S.G. 1992c. Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. *Archiv für Hydrobiologie* 125(1): 37-61.

Boulton, A.J. and Stanley, E.H. 1995. Hyporheic processes during flooding and drying in a Sonoran Desert stream. II. Faunal dynamics. *Archiv für Hydrobiologie* 134: 27-52.

Bournard, M., Cellot, B., Richoux, P. and Berrahou, A. 1996. Macroinvertebrate community structure and environmental characteristics along a large river: congruity of patterns for identification to species or family. *Journal of the North American Benthological Society* 15(2): 232-253.

Bovee, K.D. 1978. Probability-of-use criteria for the family Salmonidae. *Instream Flow Information Paper* 4. FWS/OBS-78/07. Cooperative Instream Flow Service Group. Fort Collins, Colorado, U.S.A.

Bovee, K.D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. *Instream Flow Information Paper* 12. U.S.D.I. Fish Wildl.Serv., Office of Biol. Serv. FWS/OBS-82/26: 248 pp.

Bovee, K.D. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. *Instream Flow Information Paper* 21. *U.S. Fish Wildl. Serv. Biol. Rep.* 86(7). 235 pp.

Bovee, K.D. 1996. Perspectives on two-dimensional river habitat models: the PHABSIM experience. Pp. B149-B162. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds). *Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics*. INRS-Eau, Québec, Canada.

Bovee, K.D. and Cochnauer, T. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fisheries. *Instream Flow Information Paper* 3. U.S.D.I. Fish Wildl. Serv., Office of Biol. Serv. FWS/OBS-77/63-39 pp.

Bovee, K.D. and Milhous, R. 1978. Hydraulic simulation in instream flow studies: theory and techniques. *Instream Flow Information Paper* 5. FWS/OBS-78/33. Cooperative Instream Flow Service Group. Fort Collins, Colorado.

Bovee, K.D., Gore, J.A. and Silverman, A. 1978. Field testing and adaptation of a methodology to measure 'in-stream' values in the Tongue River, Northern Great Plains (NGP) region. *Report No.* EPA-908/4-78-004A. Contract No. 68-01-2653. Office of Energy Activities, U.S. Environmental Protection Agency, Rock Mountain-Prairie Region, U.S.A.

Bovee, K.D. and Zuboy, J.R. (eds). 1988. Proceedings on a workshop on the development and evaluation of habitat suitability criteria. *U.S. Fish Wildl. Serv. Biol. Rep.* 88(11). 407 pp.

Bragg, O.M., Black, R. and Duck, R.W. 1999. Anthropogenic impacts on the hydrology of rivers and lochs. Literature review and proposed methods. Scotland and Northern Ireland Forum for Environmental Research. *Research Report* WR 98(50) I1. Scotland and Northern Ireland Forum for Environmental Research (SNIFFER), Stirling, U.K. 101 pp.

Bragg, O.M., Black, .R.A., Duck, R.W. and Rowan, J.S. 2005. Approaching the physical-biological interface in rivers: a review of methods for ecological evaluation of flow regimes. *Progress in Physical Geography* 12(29): 506-531.

Bretschko, G. and Moog, O. 1990. Downstream effects of intermittent power generation. *Water Science and Technology* 22(5): 127-135.

Brittain, J.E. and Eikeland, T.J. 1988. Invertebrate drift - a review. *Hydrobiologia* 166: 77-93.

Brittain, J.E. and Saltveit, S.J. 1989. A review of the effect of river regulation on mayflies (Ephemeroptera). *Regulated Rivers: Research & Management* 3: 191-204.

Britton, D.L., Day, J.D. and Henshall-Howard, M-P. 1993. Hydrochemical response during storm events in a South African mountain catchment: the influence of antecedent conditions. *Hydrobiologia* 250: 143-157.

Brizga, S.O. 1998. Methods addressing flow requirements for geomorphological purposes. Pp 8-46. In: Arthington, A.H. and Zalucki, J.M. (eds). Comparative evaluation of environmental flow assessment techniques: review of methods. *Land and Water Resources Research and Development Corporation Occasional Paper No*. 27/98. Canberra, Australia. 141 pp.

Brizga, S.O. 2000. Hydrology. Chapter 3: Pp. 65-85. In: Arthington, A.H., Brizga, S.O. Choy, S.C., Kennard, M.J., Mackay, S.J., McCosker, R.O., Ruffini, J.L. and Zalucki, J.M. *Environmental flow requirements of the Brisbane River downstream of Wivenhoe Dam.* South East Queensland Water Corporation, Brisbane, and Centre for Catchment and In-Stream Research, Griffith University, Brisbane, Australia. 539 pp.

Brooker, M.P. 1981. The impact of impoundments on the downstream fisheries and general ecology of rivers. Pp 91-152. In: Coaker, T.H. (ed.). *Advances in applied ecology*. *Vol.* 6. Academic Press, New York, U.S.A.

Brooker, M.P., Morris, D.L. and Hemsworth, R.J. 1977. Mass mortalities of adult salmon, *Salmo salar,* in the R. Wye, 1976. *Journal of Applied Ecology* 14: 409-417.

Brooks, S.S. and Boulton, A.J. 1991. Recolonization dynamics of benthic macroinvertebrates after artificial and natural disturbances in an Australian temporary stream. *Australian Journal of Marine & Freshwater Research* 42: 295-308.

Brown, A.V. and Brussock, P.P. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* 220: 99-108.

Brown, C.A., Eekhout, S. and King, J.M. 1996. National biomonitoring programme for riverine ecosystems: proceedings of spatial framework workshop. *NBP Report Series 2*. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Brown, C.A. and King, J.M. 2000. Volume II: IFR methodology. In: LHDA 648-F-03. Consulting services of the establishment and monitoring of the instream flow requirements for river courses downstream of LHWP Dams. Unpublished Metsi Consultants Report to Lesotho Highlands Development Authority. Metsi Consultants, Lesotho. 180 pp.

Brown, C.A and King, J.M. 2002. Breede River basin study. DRIFT application. Unpublished Technical Report. Southern Waters, Cape Town, South Africa. 80 pp.

Brown, C.A. and Joubert, A. 2003. Using multicriteria analysis to develop environmental flow scenarios for rivers targeted for water resource management. *Water SA* 29(4): 365-374.

Brunke, M., Hoffmann, A. and Pusch, M. 2001. Use of mesohabitat-specific relationships between flow velocity and river discharge to assess invertebrate minimum flow requirements. *Regulated Rivers: Research & Management* 17: 667-676.

Brusven, M.A. 1984. The distribution and abundance of benthic insects subjected to reservoir-release flows in the Clearwater River, Idaho, USA. Chapter III: Invertebrates. Pp. 167-180. In: Lillehammer, A. and Saltveit, S.J. (eds). 1984. *Regulated rivers*. Universitetsforlaget As, Oslo, Norway. 540 pp.

Bruwer, C. (ed.). 1991. *Proceedings of a Workshop on the Flow Requirements of Kruger National Park Rivers*. Department of Water Affairs and Forestry, Pretoria.

Buffagni, A. 2001. The use of benthic invertebrate production for the definition of ecologically acceptable flows in mountain rivers. Pp. 31-41. In: Acreman, M.C. (ed.). *Hydro-ecology: linking hydrology and aquatic ecology. International Association of Hydrological Sciences Publication No.* 266. IAHS Press, Centre for Ecology and Hydrology, Wallingford, U.K. 162 pp.

Bullock, A., Gustard, A. and Grainger, E.S. 1991. Instream flow requirements of aquatic ecology in two British rivers. Application and assessment of the Instream Flow Incremental Methodology using the PHABSIM system. *Report No.* 115. Institute of Hydrology, Wallingford.

Bunn, S.E. 1998. Recent approaches to assessing and providing environmental flows: concluding comments. Pp. 123-129. In: Arthington, A.H. and Zalucki, J.M. (eds). *Water for the environment: recent approaches to assessing and providing environmental flows*. Proceedings of AWWA Forum. AWWA, Brisbane, Australia. 144 pp.

Bunn, S.E. and Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30(4): 492-507.

Caissie, D. and El-Jabi, N. 1995. Comparison and regionalization of hydrologically based instream flow techniques in Atlantic Canada. *Canadian Journal of Civil Engineering* 22: 235-246.

Calow, P. 1972. A method for determining the surface area of stones to enable quantitative density estimates of littoral stone-dwelling organisms to be made. *Hydrobiologia* 40: 37-50.

Calow, P. and Petts, G.E. (eds). 1992. *The rivers handbook. Vol. 1. Hydrological and ecological principles*. Blackwell Scientific, Oxford, U.K.

Campbell, I.C. 1991. The use of macroinvertebrates to determine environmental flows in rivers and streams. Report for the Water Resources Section, Department of Conservation and Environment. Monash University, Melbourne, Australia. 40 pp.

Campbell, I.C. 1992. The feasibility of using of macroinvertebrates to determine environmental flows in Victorian rivers and streams. Report for the Department of Water Resources, Victoria. Monash University, Melbourne, Australia. 43 pp.

Canton, S.P., Cline, L.D., Short, R.A. and Ward, J.V. 1984. The macroinvertebrates and fish of a Colorado stream during a period of fluctuating discharge. *Freshwater Biology* 14: 311-316.

Car, M. 1983. The influence of water-level fluctuation on the drift of *Simulium chutteri* Lewis, 1965 (Diptera, Nematocera) in the Orange River, South Africa. *Onderstepoort Journal of Veterinary Research* 50: 173-177.

Carling, P.A. 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. *Freshwater Biology* 28: 273-284.

Carlisle, D.M. and Clements, W.H. 1999. Sensitivity and variability of metrics used in biological assessments of running waters. *Environmental Toxicology and Chemistry* 18(2): 285-291.

Carpenter, S.R. 1990. Large-scale perturbations: opportunities for innovation. *Ecology* 71(6): 2038-2043.

Carter, J.L., Fend, S.V. and Kennelly, S.S. 1996. The relationship among three habitat scales and stream benthic invertebrate community structure. *Freshwater Biology* 35(1): 109-124.

Caruso, B.S. 2002. Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of Hydrology* 257: 115-133.

Castella, E., Bickerton, M.A., Armitage, P.D. and Petts, G.E. 1995. The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia* 308: 167-182.

Castleberry, D.T., Cech, J.J. Jr., Erman, D.C., Hankin, D., Healey, M., Kondolf, G.M., Mangel, M., Mohr, M., Moyle, P.B., Nielsen, J., Speed, T.P. and Wiliams, J.G. 1996. Uncertainty and instream flow standards. *Fisheries* 21: 20-21.

Cavendish, M.G. and Duncan, M.I. 1986. Use of the instream flow incremental methodology: a tool for negotiation. *Environmental Impact Assessment Review* 6: 347-363.

Cazaubon, A. and Giudicelli, J. 1999. Impact of the residual flow on the physical characteristics and benthic community (algae, invertebrates) of a regulated Mediterranean river: the Durance, France. *Regulated Rivers: Research & Management* 15: 441-461.

Chance, M.M. and Craig, D.A. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). *Canadian Journal of Zoology* 64: 1295-1309.

Chenje, M. and Johnson, P. (eds). 1996. *Water in southern Africa*. SADC/IUCN/SARDC, Maseru/Harare. 238 pp.

Cheslak, E.F. and Garcia, J.C. 1988. An evaluation of the effects of various smoothing and curve-fitting techniques on the accuracy of suitability functions. Pp 259-286. In: Bovee, K.D. and Zuboy, J.R. (eds). Proceedings of a workshop on the development and evaluation of habitat suitability criteria. *U.S. Fish Wildl. Serv. Biol. Rep.* 88(11). 407 pp.

Cheslak, E.F. and Jacobsen, A.S. 1990. Integrating the Instream Flow Incremental Methodology with a population response model. *Rivers* 1(4): 264-288.

Chessman, B.C. 1999. Predicting the macroinvertebrate fauna of rivers by multiple regression of biological and environmental differences. *Freshwater Biology* 41(4): 747-757.

Chessman, B.C. and Robinson, D.P. 1987. Some effects of the 1982-83 drought on water quality and macroinvertebrate fauna in the lower LaTrobe River, Victoria. *Australian Journal of Marine & Freshwater Research* 38: 289-299.

Choy, S.C. 1998. Environmental flows for aquatic invertebrates. Pp. 83-92. In: Arthington, A.H. and Zalucki, J.M. (eds). *Water for the environment: recent approaches to assessing and providing environmental flows*. Proceedings of AWWA Forum. Brisbane, Australia. 144 pp.

Choy, S.C, Marshall, J.C.and Conrick, D.L. 2000. Flow requirements of aquatic invertebrates. Chapter 8: Pp. 219-264. In: Arthington, A.H., Brizga, S.O., Choy, S.C., Kennard, M.J., Mackay, S.J., McCosker, R.O., Ruffini, J.L. and Zalucki, J.M. *Environmental flow requirements of the Brisbane River downstream of Wivenhoe Dam.* South East Queensland Water Corporation, Brisbane, and Centre for Catchment and In-Stream Research, Griffith University, Brisbane, Australia. 539 pp.

Chutter, F.M. 1969. The distribution of some stream invertebrates in relation to current speed. *Internationale Revue gesamten Hydrobiologie* 54: 413-422.

Ciborowski, J.J.H., Pointing, P.J. and Corkum, L.D. 1977. The influence of current velocity and sediment on the drift of the mayfly *Ephemerella subvaria* McDunnough. *Freshwater Biology* 7: 567-572.

Ciborowski, J.J.H. 1983. Influence of current velocity, density, and detritus on drift of two mayfly species (Ephemeroptera). *Canadian Journal of Zoology* 61: 119-125.

Clarke, K.D. and Scruton, D.A. 1997. The benthic community of stream riffles in Newfoundland, Canada and its relationship to selected physical and chemical parameters. *Journal of Freshwater Ecology* 12(1): 113-121.

Clarke, K.R. and Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92: 205-219.

Clarke, K.R. and Gorley, R.N. 2001. *PRIMER v5: user manual/tutorial*. PRIMER-E Ltd., Plymouth, United Kingdom. 91 pp.

Clarke, K.R. and Warwick, R.M. 2001. *Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition*. PRIMER-E Ltd., Plymouth, United Kingdom.

Clausen, B. and Biggs, B.J.F. 1997. Relationships between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology* 38: 327-342.

Clausen, B. and Biggs, B.J.F. 2000. Flow variables for ecological studies in temperate streams; groupings based on covariance. *Journal of Hydrology* 237: 184-197.

Clinton, S.M., Grimm, N. B. and Fisher, S. G. 1996. Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society* 15: 700-712.

Cobb, D.G., Galloway, T.D. and Flannagan, J.F. 1992. Effect of discharge and substrate stability on density and composition of stream insects. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1788-1795.

Cohen, P., Andriamahefa, H. and Wasson, J.G. 1998. Towards a regionalization of aquatic habitat: distribution of mesohabitats at the scale of a large basin. *Regulated Rivers: Research & Management* 14(5): 391-404.

Coke, M. 1970. The water requirements of the Pongola floodplain pans. *Proceedings of the convention 'Water for the Future'*. Department of Water Affairs. Pretoria, South Africa.

Collins, S.L. and Glenn, S.M. 1997. Intermediate disturbance and its relationship to within-and between-patch dynamics. *New Zealand Journal of Ecology* 21(1): 103-110.

Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55: 1148-1153.

Connell, J.H. and Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist* 121(6): 789-824.

Cooper, S.D., Barmuta, L., Sarnelle, O., Kratz, K. and Diehl, S. 1997. Quantifying spatial heterogeneity in streams. *Journal of the North American Benthological Society* 16(1): 174-188.

Corkum, L.D., Pointing, P.J. and Ciborowski, J.J.H. 1977. The influence of current velocity and substrate on the distribution and drift of two species of mayflies (Ephemeroptera). *Canadian Journal of Zoology* 55: 1970-1977.

Corrarino, C.A. and Brusven, M.A. 1983. The effects of reduced stream discharge on insect drift and stranding of near-shore insects. *Freshwater Invertebrate Biology* 2: 88-98.

Cottingham, P., Stewardson, M., Roberts, J., Metzeling, L., Humphries, P., Hillman, T. and Hannan, G. 2001. Report of the Broken River scientific panel on the environmental condition and flows of the Broken River and Broken Creek. *Technical Report* 10/2001. Cooperative Research Centre for Freshwater Ecology, University of Canberra, ACT, Australia. 100 pp.

Cottingham, P., Thoms, M.C. and Quinn, G.P. 2002. Scientific panels and their use in environmental flow assessment in Australia. *Australian Journal of Water Resources* 5(1): 103-111.

Covich, A.P. 1993. Water and ecosystems. Pp. 40-55. In: Gleick, P.H. (ed.). *Water in crisis: a guide to the world's fresh water resources*. Oxford University Press, Oxford, U.K.

Covich, A.P., Shepard, W.D., Bergey, E.A. and Carpenter, C.S. 1978. Effects of fluctuating flow rates and water levels on chironomids: direct and indirect alterations of habitat stability. Pp. 141-155. In: Thorp, J.H. and Gibbons, J.W. (eds). *Energy and environmental stress in aquatic systems*. Technical Information Center, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A.

Covich, A. P., Crowl, T. A. and Scatena, F. N. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology* 48: 1199-1206.

Cowling, R.M. (ed.). 1992. *The ecology of fynbos. Nutrients, fire and diversity*. Oxford University Press, Cape Town. 411 pp.

Cowling, R. and Holmes, D. 1992. Flora and vegetation. Pp. 23-61. In: Cowling, R. (ed.). *The ecology of fynbos. Nutrients, fire and diversity*. Oxford University Press, Cape Town. 411 pp.

Cowling, R. and Richardson, D. 1995. *Fynbos. South Africa's unique floral kingdom.* Fernwood Press, Vlaeberg. 156 pp.

Cowx, I.G., Young, W.O. and Hellawell, J.M. 1984. The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology* 14: 165-177.

Craig, J.F. and Kemper, J.B. (eds). 1987. *Regulated streams: advances in ecology*. Plenum Press, New York and London, U.S.A. and U.K.

Cranston, P.S., Oliver, D.R. and Sæther, O.A. 1983. The larvae of Orthocladiinae (Diptera: Chironomidae) of the Holarctic region - keys and diagnoses. *Entomologica Scandinavica Supplement* 19: 149-291.

Crisp, D.T. 1995. The ecological basis for the management of flows regulated by reservoirs in the United Kingdom. Chapter 7. Pp. 93-103. In: Harper, D.M. and Ferguson, A.J.D. (eds*). The ecological basis for river management.* John Wiley and Sons Ltd, Chichester, U.K.

Crowder, D.W. and Diplas, P. 2000. Using two-dimensional hydrodynamic models at scales of ecological importance. *Journal of Hydrology* 230: 172-191.

Cuffney, T.F. and Wallace, J.B. 1989. Discharge-export relationships in headwater streams: the influence of invertebrate manipulations and drought. *Journal of the North American Benthological Society* 8(4): 331-341.

Cushman, R.M. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management* 5: 330-339.

Dacova, Sn., Uzunov, Y. and Mandadjiev, D. 2000. Low flow - the river's ecosystem limiting factor. *Ecological Engineering* 16: 167-174.

Dahm, C.N., Baker, M.A., Moore, D.I. and Thibault, J.R. 2003. Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology* 48: 1219-1232.

Dall, P.C. 1979. A sampling technique for littoral stone-dwelling organisms. *Oikos* 33: 106-112.

Dallas, H.F. and Day, J.A. 1993. The effect of water quality variables on riverine ecosystems: a review. *Water Research Commission Report No.* TT 61/93. Water Research Commission, Pretoria. 240 pp.

Dallas, H.F., Day, J.A. and Reynolds, E.G. 1994. The effects of water quality variables on riverine biotas. *Water Research Commission Report No.* 351/1/94. Water Research Commission, Pretoria. 230 pp.

Dallas, H.F., Day, J.A., Musibono, D.E. and Day, E.G. 1998. Water quality for aquatic ecosystems: tools for evaluating regional guidelines. *Water Research Commission Report No*. 626/1/98. 240 pp.

Dallas, M.F., Janssens, M.P. and Day, J.A. 1999. An aquatic macroinvertebrate and chemical database for riverine ecosystems. *Water SA* 25 (1): 1-8.

Davies, B.R. 1979. Stream regulation in Africa: a review. Pp: 113-142. In: Ward, J.V. and Stanford, J.A. (eds). *The ecology of regulated streams*. Plenum Press, New York and London, U.S.A. and U.K.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. A synthesis of the ecological functioning, conservation and management of South African river systems. *Water Research Commission Report No.* TT62/93. Water Research Commission, Pretoria, South Africa. 232 pp.

Davies, B.R., Thoms, M.C., Walker, K.F., O'Keeffe, J.H. and Gore, J.A. 1994. Dryland rivers: their ecology, conservation and management. Chapter 25: 484-511. In: Calow, P. and Petts, G.E. (eds). *The rivers handbook. Volume 2.* Blackwell Scientific Publications, Oxford, U.K.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1995. River and stream ecosystems in southern Africa: predictably unpredictable. Chapter 18: 537-599. In: Cushing, C.E., Cummins, K.W. and Minshall, G.W (eds). *Ecosystems of the world 22. River and stream ecosystems*. Elsevier, Amsterdam.

Davies, B.R. and Day, J.A. 1998. *Vanishing Waters*. University of Cape Town Press, Cape Town, South Africa. 487 pp.

Davies, B.R. and Wishart, M.J. 2000. River conservation in the countries of the Southern African Development Community (SADC). Chapter 7: 179-204. In: Boon, P.J., Davies, B.R. and Petts, G.E. (eds). *Global perspectives on river conservation: science, policy and practice*. John Wiley & Sons, Chichester, U.K.

Davis, J.A. 1986. Boundary layers, flow microenvironments and stream benthos. Pp 293-312. In: De Dekker, P. and Williams, W.D. (eds). *Limnology in Australia*. Australian Society for Limnology. C.S.I.R.O., Melbourne. Dr W Junk Publishers, Dordrecht, The Netherlands.

Davis, J.A. and Barmuta, L.A. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology* 21: 271-282.

Davis, J.A. and Growns, I.O. 1991. Towards defining the role of nearbed flow regimes in determining the patchiness of stream benthos. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 24: 2056-2059.

Day, J.A. 1990. Pitfalls in the presentation of chemical data. *Southern African Journal of Aquatic Sciences* 16(1/2): 1-14.

Day, J.A. and King, J.M. 1995. Geographical patterns and their origins, in the dominance of major ions in South African rivers. *South African Journal of Science* 91: 291-306.

Day, J.A., Harrison, A.D. and De Moor, I.J. (eds). 2002. Guides to the freshwater invertebrates of southern Africa. Volume 9: Diptera. *Water Research Commission Report No*. TT 201/02. Water Research Commission, Pretoria, South Africa. 200 pp.

Death, R.G. 1996a. Predicting the impacts of biological and physical disturbances: does theoretical ecology hold any answers? *New Zealand Journal of Ecology* 20(1): 17-26.

Death, R.G. 1996b. The effect of patch disturbance on stream invertebrate community structure: the influence of disturbance theory. *Oecologia* 108(3): 567-576.

Death, R.G. and Winterbourn, M.J. 1994. The measurement of environmental stability in streams: a multivariate approach. *Journal of the North American Benthological Society* 13(2): 125-139.

Death, R.G. and Winterbourn, M.J. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76(5): 1446-1460.

Death, R.G., Dewson, Z.S. and James, A.B.W. 2009. Is structure or function a better measure of the effects of water abstraction on ecosystem integrity? *Freshwater Biology* 54(10): 2037-2050.

Debinski, D.M., Ray, C. and Saveraid, E.H. 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? *Biological Conservation* 98(2): 179-190.

Delucchi, C.M. 1988. Comparison of community structure among streams with different temporal flow regimes. *Canadian Journal of Zoology* 66: 579-586.

Delucchi, C.M. 1989. Movement patterns of invertebrates in temporary and permanent streams. *Oecologia.* 78: 199-207.

De Moor, I.J., Day, J.A. and De Moor, F.C. (eds). 2003a. Guides to the freshwater invertebrates of southern Africa. Volume 7: Insecta I. Ephemeroptera, Odonata & Plecoptera. *Water Research Commission Report No*. TT 207/03. Water Research Commission, Pretoria, South Africa. 288 pp.

De Moor, I.J., Day, J.A. and De Moor, F.C. (eds). 2003b. Guides to the freshwater invertebrates of southern Africa. Volume 8: Insecta II. Hemiptera, Megaloptera, Neuroptera, Trichoptera & Lepidoptera. *Water Research Commission Report No*. TT 214/03. Water Research Commission, Pretoria, South Africa. 209 pp.

Dent, M.C., Lynch, S.D., Schulze, R.E., Seed, A.W. and Wills, H.M.M. 1989. Mapping mean annual and other rainfall statistics over southern Africa. *Water Research Commission Report No.* 109/1/89. Water Research Commission, Pretoria, South Africa.

Department of Environment Affairs and Tourism (DEAT). 1997. Broad terrain patterns and erosivity maps. Department of Environment Affairs and Tourism, Pretoria, South Africa.

Department of Water Affairs (DWA). 1986. *Management of the water resources of the Republic of South Africa*. Department of Water Affairs, Pretoria, South Africa.

Department of Water Affairs (DWA). 1990. List of hydrological gauging stations. *Hydrological Information Publication No.* 15. July 1990. Volume 1. Gauging stations in flowing water. Directorate of Hydrology, Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 1991. Flow gauging stations: calibration and evaluation. Volume VIII. Prepared by Rooseboom, A., Basson, G.R. and Carter, C.A. Ninham Shand Inc. in association with BKS Inc. *Department of Water Affairs and Forestry Report No*. P G000/00/1090. Department of Water Affairs and Forestry, Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 1994. Hydrology of the Riviersonderend basin, upper Molenaars and Elandspad River. George, W. and Dunn, P., Ninham Shand Inc., in association with BKS Inc. Final Report for Western Cape System Analysis. Department of Water Affairs and Forestry Report No. P G000/00/2791. Department of Water Affairs and Forestry, Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 1997. Skuifraam feasibility study. Hydrology. Larsen, J., Ninham Shand Consulting Engineers. *Department of Water Affairs and Forestry Report* No. PG100/00/0797. Department of Water Affairs and Forestry, Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 1999a. *Resource directed measures for protection of water resources*. *Volume 2: integrated manual. Version 1.0.* Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 1999b. *Resource directed measures for protection of water resources*. *Volume 3: river ecosystems. Version 1.0.* Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Dewson, Z.S., Death, R.G. and James, A.B.W. 2003. The effect of water abstractions on invertebrate communities in four small North Island streams. *New Zealand Natural Sciences* 28: 51-65.

Dewson, Z.S., James, A.B.W. and Death, R.G. 2007a. Invertebrate community responses to experimentally reduced discharge in small streams of different water quality. *Journal of the North American Benthological Society* 26(4):754-766.

Dewson, Z. S., James, A.B.W. and Death, R.G. 2007b. Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology* 52:357-369.

Dewson, Z.S., James, A.B.W. and Death, R.G. 2007c. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* 26(3): 401-415.

Docampo, L. and De Bikuña, B.G. 1993. The Basque method for determining instream flows in northern Spain. *Rivers* 4(4): 292-311. (Also cited as 1995).

Doeg, T.J. and Lake, P.S. 1981. A technique for assessing the composition and density of the macroinvertebrate fauna of large stones in streams. *Hydrobiologia* 80: 3-6.

Doeg, T.J., Lake, P.S. and Marchant, R. 1989. Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. *Australian Journal of Ecology* 14: 207-220.

Dolédec, S., Statzner, B. and Bournard, M. 1999. Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology* 42: 737-758.

Dole-Olivier, M.J., Marmonier, P. and Beffy, J. L. 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biology* 37: 257-276.

Downes, B.J. 1990. Patch dynamics and mobility of fauna in streams and other habitats. *Oikos* 59: 411-413.

Downes, B.J., Lake, P.S. and Schreiber, E.S.G. 1993. Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. *Freshwater Biology* 30: 119-132.

Downes, B.J., Lake, P.S., Glaister, A and Webb, J.A. 1998a. Scales and frequencies of disturbance: rock size, bed packing and variation among upland streams. *Freshwater Biology* 40: 625-639.

Downes, B.J., Lake, P.S., Schreiber, E.S.G. and Glaister, A. 1998b. Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs* 68(2): 237-257.

Dudgeon, D. 1992a. Endangered ecosystems: a review of the conservation status of tropical Asian rivers. *Hydrobiologia* 248: 167-191.

Dudgeon, D. 1992b. Effects of water transfer on aquatic insects in a stream in Hong Kong. *Regulated Rivers: Research & Management* 7: 369-377.

Dudgeon, D. 1993. The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshwater Biology* 30: 189-197.

Dudgeon, D. 2000. Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity. *BioScience* 50(9): 793-806.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A., Soto, D., Stiassny, M.L.J. and Sullivan, C.A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163-182.

Dunbar, M.J., Gustard, A., Acreman, M. C. and Elliott, C.R.N. 1998. Review of overseas approaches to setting river flow objectives. *Environment Agency RandD Technical Report* W6B(96)4. Institute of Hydrology, Wallingford, U.K. 80 pp.

Dunbar, M.J. and Acreman, M.C. 2001. Applied hydro-ecological science for the twenty-first century. Pp. 1-17. In: Acreman, M.C. (ed.). Hydro-ecology: linking hydrology and aquatic ecology. *International Association of Hydrological Sciences Publication No.* 266. IAHS Press, Centre for Ecology and Hydrology, Wallingford, U.K. 162 pp.

Dunbar, M.J., Acreman, M.C. and Kirk, S. 2004. Environmental flow setting in England and Wales: strategies for managing abstraction in catchments. *Journal of the Chartered Institution of Water and Environmental Management* 18(1): 5-10.

Dyer, T.G.J. 1976. Expected future rainfall over selected parts of South Africa. *South African Journal of Science* 72: 237-239.

Dynesius, M. and Nilsson, C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266: 753-762.

Dyson M, Bergkamp, G. and Scanlon, J (eds). 2003. *Flow. The essentials of environmental flows.* IUCN, Gland, Switzerland and Cambridge, U.K. xiv + 118 pp.

Edington, J.M. 1965. The effect of water flow on populations of net-spinning Trichoptera. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 13: 40-48.

Edington, J.M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *Journal of Animal Ecology* 37: 675-692.

Eekhout, S., King, J.M. and Wackernagel, A. 1997. *Classification of South African rivers. Volume 1.* Main Report for Department of Environment Affairs and Tourism. Freshwater Research Unit, University of Cape Town, South Africa. 125 pp.

Emery, A.J. 1994. A preliminary study into the effect of spates on the species composition and abundance of benthic macroinvertebrate assemblages on rocks in two biotopes in a Cape mountain stream. Unpublished B.Sc. (Honours) Thesis. Department of Zoology, University of Cape Town, Cape Town, South Africa.

Englund, G. and Malmqvist, B. 1996. Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in North Swedish rivers. *Regulated Rivers: Research & Management* 12: 433-445.

Espegren, G.D. 1998. Evaluation of the standards and methods used for quantifying instream flows in Colorado. Final Report. Colorado Water Conservation Board. Denver, Colorado, U.S.A. 18 pp.

Estes, C.C. 1996. Annual summary of instream flow reservations and protection in Alaska. Alaska Department of Fish and Game. *Fisheries Data Series No*. 96-45. Anchorage, Alaska, U.S.A. 106 pp.

Everard, M. 1996. The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum* 7: 33-50.

Everett, M.J. and Quibell, G. 1995. The feasibility of using a physiographic approach in water quality management. Phase II – Protocols towards physiographic boundary verification, using the Eastern Transvaal regions as an example. *Internal Report No*. N/0000/00//REQ/0794. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Extence, C.A. 1981. The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia* 83: 217-224.

Extence, C.A., Balbi, D.M. and Chadd, R.P. 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. *Regulated Rivers: Research & Management* 15: 543-574.

Falkenmark, M. 2003. Water management and ecosystems: living with change. *TEC Background Papers No*. 9. Global Water Partnership, Stockholm, Sweden.

Feminella, J. W. 1996. Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. *Journal of the North American Benthological Society* 15(4): 651-669.

Feminella, J.W. and Resh, V.H. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. *Ecology* 71(6): 2083-2094.

Ferrar, A.A. (ed.). 1989. Ecological flow requirements for South African rivers. *South African National Scientific Programmes Report No.* 162. Foundation for Research Development, CSIR, Pretoria. 118 pp.

Field, J.G., Clarke, K.R. and Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.

Fisher, S.G. 1983. Succession in streams. Pp. 7-27. In: Barnes, J.R. and Minshall, G.W. (eds). *Stream ecology. Application and testing of general ecological theory*. Plenum Press, New York, U.S.A. 399 pp.

Fisher, S.G. 1987. Succession, scale and hypothesis testing in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 689-691.

Fisher, S.G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. *Environmental Management*14: 725-736.

Fisher, S.G., Gray, L.J., Grimm, N.B. and Busch, D.E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52(1): 93-110.

Fisher, S.G. and Grimm, N.B. 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1183-1189.

Fisher, S.G. and Grimm, N.B. 1991. Streams and disturbance: are cross-ecosystem comparisons useful? Chpt. 10: 196-221. In: Cole, J.C., Lovett, G.M. and Findlay, S.E.G. (eds). *Comparative analysis of ecosystems: patterns, mechanisms, and theories.* Proceedings of the third Cary conference in ecosystem science. Springer-Verlag, New York, NY, U.S.A.

Fonseca, D.M. and Hart, D.D. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* 75: 49-56.

Frid, C.L.J. and Townsend, C.R. 1989. An appraisal of the patch dynamics concept in stream and marine benthic communities whose members are highly mobile. *Oikos* 56: 137-141.

Frissell, C.A., Liss, W.J., Warren, C.E. and Hurley, M.D. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10(2): 199-214.

Gan, K.C. and McMahon, T.A. 1990a. Variability of results from the use of PHABSIM in estimating habitat area. *Regulated Rivers: Research & Management* 5: 233-239.

Gan, K.C. and McMahon, T.A. 1990b. Comparison of two computer models for assessing environmental flow requirements. *Centre for Environmental Applied Hydrology Report*. University of Melbourne, Victoria, Australia. 104 pp.

Gan, K.C., McMahon, T.A. and Finlayson, B.L. 1991. Analysis of periodicity in streamflow and rainfall data by Colwell's indices. *Journal of Hydrology* 123: 105-118.

Ghanem, A., Steffler, P., Hicks, F. and Katopodis, C. 1996. Two-dimensional hydraulic simulation of physical habitat conditions in flowing streams. *Regulated Rivers: Research & Management* 12: 185-200.

Ginot, V. 1995. EVHA. Un logiciel d'evaluation de l'habitat du poisson sous Windows. *Bulletin Français de la Pêche et de la Pisciculture* 337-338-339: 303-308.

Gippel, C.J. 2001. Australia's environmental flow initiative: filling some knowledge gaps and exposing others. *Water Science and Technology* 43(9): 73-88.

Gippel, C.J., Stewardson, M.J., Jayasuriya, M.D.A., Finlayson, B.L. and McMahon, T.A. 1994. Development of an holistic flow management strategy for the Thomson River, Victoria. Pp. 111-118. In: *Environmental flows seminar proceedings*. AWWA Inc., Artarmon, Australia.

Gippel, C.J. and Stewardson, M.J. 1998. Use of wetted perimeter in defining minimum environmental flows. *Regulated Rivers: Research & Management* 14: 53-67.

Glasby, T.M. and Underwood, A.J. 1996. Sampling to differentiate between pulse and press perturbations. *Environmental Monitoring and Assessment* 42: 241-252.

Gleick, P.H. 1993. Water in the 21st century. Pp: 105-113. In: Gleik, P.H. (ed.). *Water in crisis*. Oxford University Press, Oxford.

Gleick, P.H. 2000. Water futures: a review of global water resources projections. Pp. 27-45. In: Rijsberman, F.R. (ed). *World water scenarios.* Earthscan, London, U.K.

Glozier, N.E. and Culp, J.M. 1989. Experimental investigations of diel vertical movements by lotic mayflies over substrate surfaces. *Freshwater Biology* 21: 253-260.

Godbout, L. and Hynes, H.B.N. 1982. The three dimensional distribution of the fauna in a single riffle in a stream in Ontario. *Hydrobiologia* 97: 87-96.

Goetsch, P.-A. and Palmer, C.G. 1997. Salinity tolerances of selected macroinvertebrates of the Sabie River, Kruger National Park, South Africa. *Archives of Environmental Contamination and Toxicology* 32(1): 32-41.

Golterman, H.L., Clymo, R.S. and Ohnstad, M.A.M. 1978. *IBP Handbook No. 8. Methods for physical and chemical analysis of fresh waters. Second edition*. Blackwell Scientific Publications, Oxford, U.K.

Gordon, N.D., McMahon, T.A. and Finlayson, B.L. 1992. *Stream hydrology. An introduction for ecologists*. John Wiley and Sons, Chichester, U.K. 526 pp.

Gore, J.A. 1977. Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia* 55(2): 113-123.

Gore, J.A. 1978. A technique for predicting instream flow requirements of benthic macroinvertebrates. *Freshwater Biology* 8: 141-151.

Gore, J.A. 1987. Development and application of macroinvertebrate instream flow models for regulated flow management. In: Craig, J.F. and Kemper, J.B. (eds). *Regulated streams: advances in ecology*. Plenum Press, New York and London, U.S.A. and U.K.

Gore, J.A. 1989. Models for predicting benthic macroinvertebrate habitat suitability under regulated flows. Pp 253-265. In: Gore, J.A. and Petts, G.E. (eds). 1989. *Alternatives in regulated river management*. CRC Press, Inc., Florida, U.S.A.

Gore, J.A. 1996. Responses of aquatic biota to hydrological change. Pp. 209-230. In: Petts, G.E. and Calow, P. (eds). *River biota. Diversity and dynamics*. Blackwell Science Publications, Oxford, U.K.

Gore, J.A. 1998. Instream flow studies and habitat suitability - criteria for macroinvertebrates. Pp. 14-16. In: Blažková, Š., Stalnaker, C. and Novický, O. (eds). *Hydroecological modelling. Research, practice, legislation and decision-making*. Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Gore, J.A. and Judy, R.D.Jr. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1363-1370.

Gore, J.A. and Nestler, J.M. 1988. Instream flow studies in perspective. *Regulated Rivers: Research & Management* 2: 93-101.

Gore, J.A. and King, J.M. 1989. Application of the revised physical habitat simulation (PHABSIM II) to minimum flow evaluations of South African rivers. In: Kienzle, S. and Maaren, H. (eds). *Proceedings of the fourth South African National Hydrological Symposium*. 20-22 November. Pretoria, South Africa. 447 pp.

Gore, J.A. and Petts, G.E. (eds). 1989. *Alternatives in regulated river management*. CRC Press, Inc., Florida, U.S.A.

Gore, J.A., Nestler, J.M. and Layzer, J.B. 1990. Habitat factors in tailwaters with emphasis on peaking hydropower. *Technical Report* EL-90-2. US Army Engineer Waterways Experiment Station, Vicksburg, MS, U.S.A. 90 pp.

Graham, A.A., McCaughan, D.J. and McKee, F.S. 1988. Measurement of surface area of stones. *Hydrobiologia* 157: 85-87.

Gray, L.J. and Fisher, S.G. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *The American Midland Naturalist* 106(2): 249-257.

Gray, N.F. 1985. Heterotrophic slimes in flowing waters. *Biological Reviews* 60: 499-548.

Green Cross International (GCI). 2000. *National sovereignty and international watercourses*. Ruckstuhl SA, Renens, Switzerland. 144 pp.

Grenney, W.J., Porcella, D.B. and Cleave, M.L. 1976. Water quality relationships to flow - streams and estuaries. In: Stalnaker, C.B. and Arnette, S.C. (eds). *Methodologies for the determination of stream resource flow requirements: an assessment.* U.S. Fish and Wildlife Services, Office of Biological Services Western Water Association, U.S.A. 199 pp.

Grimm, N.B. 1994. Disturbance, succession and ecosystem processes in streams: a case study from the desert. Pp. 93-112. In: Giller, P.S., Hildrew, A.G. and Raffaelli, D.G. (eds). *Aquatic ecology. Scale, pattern and process.* The 34th Symposium of the British Ecological Society with the American Society of Limnology and Oceanography. University College, Cork, 1992. Blackwell Science Publications, Oxford, U.K. 649 pp.

Grimm, N.B. and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8: 293-307.

Groombridge, B. and Jenkins, M.D. 2002. Inland water biodiversity. Chapter 7: Pp 163-194. In: *World atlas of biodiversity. Earth's living resources in the 21st Century*. Prepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkley, U.S.A. 340 pp.

Groshens, T.P. and Orth, D.J. 1994. Transferability of habitat suitability criteria for smallmouth bass, *Micropterus dolomieu*. *Rivers* 4(3): 194-212.

Growns, I.O. 1998. Methods addressing the flow requirements of aquatic invertebrates. Pp. 115-140. In: Arthington, A.H., and Zalucki, J.M. (eds). Comparative evaluation of environmental flow assessment techniques: review of methods. *Land and Water Resources Research and Development Corporation Occasional Paper No*. 27/98. Canberra, Australia.

Growns, I.O. and Kotlash, A. 1994. Environmental flow allocations for the Hawkesbury-Nepean River system: a review of information. *Australian Water Technologies EnSight Report No*. 94/189. Australia. 55 pp.

Growns, J. and Marsh, N. 2000. Characterisation of flow in regulated and unregulated streams in eastern Australia. *Cooperative Research Centre for Freshwater Ecology Technical Report* 3/2000. Elect Printing, ACT, Australia. 66 pp.

Growns, I.O. and Growns, J.E. 2001. Ecological effects of flow regulation on macroinvertebrate and periphytic diatom assemblages in the Hawkesbury-Nepean River, Australia. *Regulated Rivers: Research & Management* 17: 275-293.

Gurtz, M.E. and Wallace, J.B. 1984. Substrate-mediated response of stream invertebrates to disturbance. *Ecology* 65: 1556-1569.

Gustard, A. 1979. The characterisation of flow regimes for assessing the impact of water resource management on river ecology. Pp: 53-60. In: Ward, J.W. and Stanford, J.A. (eds). *The ecology of regulated streams*. Plenum Press, New York and London, U.S.A. and U.K.

Gustard, A. and Bullock, A. 1991. Advances in low flow estimation and impact assessment. Pp. 2.73-2.80. In: BHS 3rd National Hydrology Symposium, Southampton, 1991. *Symposium Proceedings*. Southampton, England.

Gustard, A. and Elliott, C.R.N. 1998. The application of hydro-ecological modelling in the UK. Pp. 23-31. In: Blažková, Š., Stalnaker, C. and Novický, O. (eds). *Hydroecological modelling. Research, practice, legislation and decision-making*. Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Haddad, P.R. and Jackson, P.E. 1990. Ion chromatography. Principles and applications. *Journal of Chromatography Library* 46. Elsevier, Amsterdam, The Netherlands. 751 pp.

Haines, A.T., Finlayson, B.L. and McMahon, T.A. 1988. A global classification of river regimes. *Applied Geography* 8: 255-272.

Hannah, D.M., Wood, P.J. and Sadler, J.P. 2004. Ecohydrology and hydroecology: a 'new paradigm'? *Hydrological Processes* 18: 3439-3445.

Hansen, R.A, Hart, D.D and Merz, R.A. 1991. Flow mediates predator-prey interactions between triclad flatworms and larval blackflies. *Oikos* 60: 187-196.

Hardy, T.B. 1998. The future of habitat modeling and instream flow assessment techniques. *Regulated Rivers: Research & Management* 14: 405-420.

Harper, D.M., Smith, C.D. and Barham, P.J. 1992. Habitats as the building blocks for river conservation assessment. Pp 311-319. In: Boon, P.J., Calow, P. and Petts, G.E. (eds). *River conservation and management*. John Wiley and Sons, Chichester, U.K.

Harper, D. and Everard, M. 1998. Why should the habitat-level approach underpin holistic river survey and management? *Aquatic Conservation: Marine and Freshwater Ecosystems* 8: 395-413.

Harrel, R.C. and Dorris, T.C. 1968. Stream order, morphometry, physicochemical conditions and community structure of benthic macroinvertebrates in an intermittent stream system. *American Midland Naturalist* 80: 220-251.

Harris, G.P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, and models, and management. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 877-900.

Harrison, A.D. 1965. River zonation in southern Africa. *Archiv für Hydrobiologie* 61: 380-386.

Harrison, A.D. 1966. Recolonisation of a Rhodesian stream after drought. *Archiv für Hydrobiologie* 62(3): 405-421.

Harrison, A.D. 2000. Four new genera and species of Chironomidae (Diptera) from southern Africa. *Aquatic Insects* 22(3): 219-236.

Harrison, A.D. and Agnew, J.D. 1962. The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. *Annals of the Cape Provincial Museums* 2: 273-291.

Harrison, G.W. 1979. Stability under environmental stress: resistance, resilience, persistence, and variability. *The American Naturalist* 113(5): 659-669.

Hart, D.D., Clark, B.D. and Jasentuliyana, A. 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography* 41: 297-308.

Hart, D.D. and Finelli, C.M. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* 30: 363-395.

Hauer, F.R. Stanford, J.A. and Ward, J.V. 1989. Serial discontinuities in a Rocky Mountain river. II. Distribution and abundance of Trichoptera. *Regulated Rivers: Research & Management* 3: 177-182.

Hawkins, C.P., Kershner, J.L., Bisson, P.A., Bryant, M.D., Decker, L.M., Gregory, S.V., McCullough, D.A., Overton, C.K., Reeves, G.H., Steedman, R.J. and Young, M.K. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18(6): 3-12.

Heeg, J. and Breen, C.M. 1982. Man and the Pongola floodplain. *S. Afr. Nat. Sci. Prog. Rep. No.* 56. Council for Scientific and Industrial Research, Pretoria, South Africa.

Heritage, G.L., Van Niekerk, A.W. and Weeks, D. 1996. A model of fish assemblage response to hydraulic and fluvial geomorphological change in a pool-rapid channel type. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds). Ecohydraulics 2000. *Proceedings of the 2nd International Symposium on Habitat Hydraulics.* Québec, June 1996. INRS-Eau, Québec City, Canada.

Herricks, E.E. and Braga, M.I. 1987. Habitat elements in river basin management and planning. *Water Science and Technology* 19(9): 19-29.

Hildrew, A.G. and Townsend, C.R. 1987. Organization in freshwater benthic communities. Pp. 47-371. In: Gee, J.H.R. and Giller, P.S. (eds). *Organization of communities past and present*. Blackwell Scientific, Oxford, England.

Hildrew, A.G. and Giller, P.S. 1994. Patchiness, species interactions and disturbance in the stream benthos. Pp. 21-62. In: Giller, P.S., Hildrew, A.G. and Raffaelli, D.G. (eds). *Aquatic ecology. Scale, pattern and process.* The 34th Symposium of the British Ecological Society with the American Society of Limnology and Oceanography. University College, Cork, 1992. Blackwell Science Publications, Oxford. 649 pp.

Hill Kaplan Scott Consulting Engineers (HKS). 1988. Du Toit's Kloof environmental impact assessment. Volumes 1 and 2. *N.T.C. Project No*. 1-012-04.

Hill, M.T., Platts, W.S. and Beschta, R.L. 1991. Ecological and geomorphological concepts for instream and out-of-channel flow requirements. *Rivers* 2(3): 198-210.

Hollands, J.R. 1998. A search for the link between wetted perimeter and easily computed hydrological indices of baseflow characteristics. Chapter 12: Pp. 345-355. In: King, J.M. and Tharme, R.E. Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa. *Water Research Commission Report No*. 295/1/94. Water Research Commission, Pretoria. 590 pp.

Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology, Evolution, and Systematics* 4: 1-23.

Hooper, F.F. and Ottey, D.R. 1982. Prediction of effects of daily flow fluctuations on stream biota. Institute of Water Research Completion Report. Michigan State University, East Lansing. December 1982. Draft Report for Office of Water Research and Technology. Washington, D.C. Water Resources Scientific Information Center, U.S. Department of the Interior, Washington, D.C., U.S.A. 45 pp.

Hooper, F.F. and Ottey, D.R. 1988. Responses of macroinvertebrates of two headwater streams to discharge fluctuations. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1159-1166.

Hughes, D.A. 1999. Towards the incorporation of magnitude-frequency concepts into the Building Block Methodology used for quantifying ecological flow requirements of South African rivers. *Water SA* 25(3): 279-284.

Hughes, D.A. 2001. Providing hydrological information and data analysis tools for the determination of ecological instream flow requirements for South African rivers. *Journal of Hydrology* 241: 140-151.

Hughes, D.A., O'Keeffe, J.H., Smakhtin, V. and King, J.M. 1997. Development of an operating rule model to simulate time series of reservoir releases for instream flow requirements. *Water SA* 23(1): 21-30.

Hughes, D.A. and Ziervogel, G. 1998. The inclusion of operating rules in a daily reservoir simulation model to determine ecological reserve releases for river maintenance. *Water SA* 24(4): 293-302.

Hughes, D.A. and Münster, F. 2000. Hydrological information and techniques to support the determination of the water quantity component of the ecological reserve for rivers. *Water Research Commission Report No.* 867/3/2000. Water Research Commission, Pretoria, South Africa.

Hughes, D.A. and Hannart, P. 2003. A desktop model used to provide an initial estimate of the ecological instream flow requirements of rivers in South Africa. *Journal of Hydrology* 270: 167-181.

Hughes, J.M.R. 1987. Hydrological characteristics and classification of Tasmanian rivers. *Australian Geographical Studies* 25: 61-82.

Hughes, J.M.R. and James, B. 1989. A hydrological regionalisation of streams in Victoria, Australia, with implications for stream ecology. *Australian Journal of Marine & Freshwater Research* 40: 303-326.

Humphries, P. and Baldwin, D. S. 2003. Drought and aquatic ecosystems: an introduction. *Freshwater Biology* 48: 1141-1146.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54(2): 187-211.

Hynes, H.B.N. 1958. The effect of drought on the fauna of a small mountain stream in Wales. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 13: 826-833.

Hynes, H.B.N. 1970. *The ecology of running waters*. *2nd. ed.* University of Toronto Press, Toronto. 555 pp.

Imbert, J.B. and Perry, J.A. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* 436: 191-208.

Iversen, T.M., Wiberg-Larsen, P., Birkholm Hansen, S. and Hansen, F.S. 1978. The effect of partial and total drought on the macroinvertebrate communities of three small Danish streams. *Hydrobiologia* 60(3): 235-242.

James, A.B.W., Dewson, Z.S. and Death, R.G. 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications* 24:22-35.

James, A.B.W., Dewson, Z.S. and Death, R.G. 2009. The influence of flow reduction on macroinvertebrate drift density and distance in three New Zealand streams. *Journal of the North American Benthological Society* 28(1): 220-232.

Janauer, G.A. 2000. Ecohydrology: fusing concepts and scales. *Ecological Engineering* 16(1): 9-16.

Jansson, R., Nilsson, C., Dynesius, M. and Andersson, E. 2000. Effects of river regulation on river-margin vegetation: a comparison of eight boreal rivers. *Ecological Applications* 10(1): 203-224.

Jensen, F. and Jensen, C.F. 1984. Responses of the benthic fauna to short-term lowerings of the water level in a lowland stream in Denmark. Chapter 3; 181-188. In: Lillehammer, A. and Saltveit, S.J. (eds). *Regulated rivers*. Universitetsforlaget AS, Oslo, Norway.

Jewitt, G.P.W, Hawkins, B.G. and Thiel, C. 1999. Indicators of hydrologic alteration for South African rivers. *Proceedings of Ninth South African National Hydrology Symposium*. University of the Western Cape, Cape Town, South Africa.

Jewitt, G.P.W., Weeks, D.C., Heritage, G.L. and Görgens, A.H.M. 2001. Modelling abiotic-biotic links in the rivers of the Kruger National Park, Mpumalanga, South Africa. In: Acreman, M.C. (ed.). Hydro-ecology: linking hydrology and aquatic ecology. *International Association of Hydrological Sciences Publication No.* 266. IAHS Press, Centre for Ecology and Hydrology, Wallingford, U.K. 162 pp.

Johnson, S.L. and Covich, A.P. 2000. The importance of night-time observations for determining habitat preferences of stream biota. *Regulated Rivers: Research & Management* 16: 91-99.

Jorde, K. 1996. Ecological evaluation of instream flow regulations based on temporal and spatial variability of bottom shear stress and hydraulic habitat quality. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds*). Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics.* Québec, June 1996. Volume B. INRS-Eau, Québec, Canada.

Jorde, K. and Bratrich, C. 1998. River bed morphology and flow regulations in diverted streams: effects on bottom shear stress patterns and hydraulic habitat. Pp. 47-63. In: Bretschko, G. and Helešic, J. (eds). *Advances in river bottom ecology*. Backhuys Publishers, Leiden, The Netherlands.

Jorde, K., Schneider, M., Peter, A. and Zoellner, F. 2001. Fuzzy based models for the evaluation of fish habitat quality and instream flow assessment. *CD-ROM Proceedings of the 3rd International Symposium on Environmental Hydraulics*. 5-8 December 2001, Tempe, Arizona, U.S.A.

Joubert, A.R. and Hurly, P.R. 1994. The use of daily flow data to classify South African rivers. Chapter 11: Pp. 286-359. In: King, J.M. and Tharme, R.E. Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa. *Water Research Commission Report No.* 295/1/94. Water Research Commission, Pretoria, South Africa. 590 pp.

Jowett, I.G. 1989. River hydraulic and habitat simulation, RHYHABSIM computer manual. *Fisheries Miscellaneous Report* 49. New Zealand Ministry of Agriculture and Fisheries, Christchurch, New Zealand. 39 pp.

Jowett, I.G. 1993. A method for objectively identifying pool, run, and riffle habitats from physical measurements. *New Zealand Journal of Marine and Freshwater Research* 27: 241-248.

Jowett, I.G. 1997. Instream flow methods: a comparison of approaches. *Regulated Rivers: Research & Management* 13: 115-127.

Jowett, I.G. 1998. Hydraulic geometry of New Zealand rivers and its use as a preliminary method of habitat assessment. *Regulated Rivers: Research & Management* 14: 451-466.

Jowett, I.G. 2003. Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed rivers. *River Research and Applications* 19: 495-507.

Jowett, I.G. and Duncan, M.J. 1990. Flow variability in New Zealand rivers and its relationship to instream habitat and biota. *New Zealand Journal of Marine and Freshwater Research* 24: 305-317.

Jowett, I.G. and Richardson, J. 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. *New Zealand Journal of Marine and Freshwater Research* 24: 19-30.

Jowett, I.G., Richardson, J., Biggs, B.J.F., Hickey, C.W. and Quinn, J.M. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 25: 187-199.

Junk, W.J., Bayley, P.B. and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. Proceedings of the International Large River Symposium (LARS). *Canadian Special Publications in Fisheries and Aquatic Sciences* 106: 110-127.

Kamler, E. and Reidel, W. 1960. The effect of drought on the fauna, Ephemeroptera, Plecoptera and Trichoptera of a mountain stream. *Polskie Archiwum Hydrobiologii.* 8: 87-94.

Karim, K., Gubbels, M.E. and Goulter, I.C. 1995. Review of determination of instream flow requirements with special application to Australia. *Water Resources Bulletin* 31(6).

Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. *Ecological Applications* 1: 66-84.

Kay, W.R., Smith, M.J., Pinder, A.M., McRae, J.M., Davis, J.A. and Halse, S.A. 1999. Patterns of distribution of macroinvertebrate families in rivers of north-western Australia. *Freshwater Biology* 41(2): 299-316.

Kemp, J.L., Harper, D.M. and Crosa, G.A. 1999. Use of 'functional habitats' to link ecology with morphology and hydrology in river rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9: 159-178.

Kemp, J.L., Harper, D.M. and Crosa, G.A. 2000. The habitat-scale ecohydraulics of rivers. *Ecological Engineering* 16(1): 17-29.

Kershner, J.L. and Snider, W.M. 1992. Importance of a habitat-level classification system to design instream flow studies. Chapter 12: Pp. 179-193. In: Boon, P.J., Calow, P. and Petts, G.E. (eds). *River conservation and management.* John Wiley and Sons, Chichester, U.K.

Kershner, J.L., Snider, W.M., Turner, D.M. and Moyle, P.B. 1992. Distribution and sequencing of mesohabitats: are there differences at the reach scale? *Rivers* 3(3): 179-190.

King, J.M. 1981. The distribution of invertebrate communities in a small South African river. *Hydrobiologia* 83: 43-65.

King, J.M., Day, J.A. and Van Der Zel, D.W. 1979. Hydrology and hydrobiology. In: Day, J., Siegfried, W.R., Louw, G.N. and Jarman, M.L. (eds). Fynbos ecology: a preliminary synthesis. *South African National Scientific Programmes Report No.* 40. 166 pp.

King, J.M., Davies, B.R. and Day, J.A. 1986. The way things were -rivers natural and not so natural. In: Davies, B.R. and Day, J.A. *The biology and conservation of South Africa's vanishing waters*. The Centre for Extra-mural Studies, University of Cape Town, South Africa.

King, J.M. and O'Keeffe, J.H. 1989. Looking to the future - South Africa's requirements. In: Ferrar, A.A. (ed.). 1989. Ecological flow requirements for South African rivers. *South African National Scientific Programmes Report No.* 162. Foundation for Research Development, CSIR, Pretoria, South Africa. 118 pp.

King, J.M., De Moor, F.C. and Chutter, F.M. 1992. Alternative ways of classifying rivers in South Africa. Chpt. 14: 213-228. In: Boon, P.J., Calow, P. and Petts, G.E. (eds). *River conservation and management*. John Wiley and Sons, Chichester, U.K.

King, J.M. and Tharme, R.E. 1993. River ecologists need hydrological information for assessing environmental water allocations, but what form should it take and why? Pp. 665-671. In: Lorentz, S.A., Kienzle, S.W., and Dent, M.C. (eds). *Proceedings of the sixth South African national hydrological symposium. "Hydrology in developing regions...The road ahead"*. Volume II. 8-10 September 1993. Department of Agricultural Engineering, University of Natal, Pietermaritzburg, South Africa.

King, J.M. and Tharme, R.E. 1994. Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa. *Water Research Commission Report No.* 295/1/94. Water Research Commission, Pretoria, South Africa. 590 pp.

King, J.M., O'Keeffe, J.H., Pollard, S., Tharme, R.E. and Weeks, D. 1995. Assessment of environmental water requirements for selected South African rivers: problems and possible approaches. *Water Research Commission Report No*. KV 72/95. Water Research Commission, Pretoria, South Africa. 58 pp.

King, J.M. and Louw, M.D. 1998. Instream flow assessments for regulated rivers in South Africa using the Building Block Methodology. *Aquatic Ecosystem Health and Management* 1: 109-124.

King, J.M., Cambray, J.A. and Impson, D.N. 1998. Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish *Barbus capensis*. *Hydrobiologia* 384: 245-265.

King, J.M., Tharme, R.E. and Brown, C.A. 1999. Definition and implementation of instream flows. *Thematic Report for the World Commission on Dams*. Southern Waters Ecological Research and Consulting. Cape Town, South Africa. 63 pp.

King, J.M., Tharme, R.E. and De Villiers, M.S. (eds). 2000. Environmental flow assessments for rivers: manual for the Building Block Methodology. *Water Research Commission Technology Transfer Report No.* TT131/00. Water Research Commission, Pretoria, South Africa. 340 pp.

King, J.M. and Schael, D.M. 2001. Assessing the ecological relevance of a spatially-nested geomorphological hierarchy for river management. *Water Research Commission Report No.* 754/1/01. Water Research Commission, Pretoria, South Africa. 276 pp; A-68 pp.

King, J.M., Brown, C.A and Sabet, H. 2003. A scenario-based holistic approach to environmental flow assessments for rivers. *River Research and Applications* 19: 619-639.

King, L.C. 1963. *South African scenery. A textbook of geomorphology*. *Third edition*. Oliver and Boyd, London, U.K.

Kingsford, R.T. 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology* 25: 109-127.

Konrad, C.P., Brasher, A.M.D. and May, J.T. 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biology* 53: 1983-1998.

Kotliar, N.B. and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260.

Kownacki, A. 1985. Effect of droughts on the macroinvertebrate communities of high mountain streams. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 2069-2072.

Kraft, M.E. 1972. Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada* 29(10): 1405-1411.

Krebs, C.J. 1985. *Ecology: the experimental analysis of distribution and abundance*. *Third edition*. Harper & Row, Publishers, Inc., New York, U.S.A. 800 pp.

Kroger, R.L. 1973. Biological effects of fluctuating water levels in the Snake River, Grand Teton National Park, Wyoming. *American Midland Naturalist* 89: 478-481.

Ladle, M. and Bass, J.A.B. 1981. The ecology of a small chalk stream and its responses to drying during drought conditions. *Archiv für Hydrobiologie* 90: 448-466.

Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19: 573-592.

Lake, P.S. 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* 48: 1161-1172.

Lake, P.S. and Doeg, T.J. 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. *Hydrobiologia* 126: 199-211.

Lake, P.S., Doeg, T.J., and Marchant, R. 1989. Effects of multiple disturbance on macroinvertebrate communities in the Acheron River, Victoria. *Australian Journal of Ecology* 14: 507-514.

Lamb, B.L. 1989. Comprehensive technologies and decision-making: reflection on the instream flow incremental methodology. *Fisheries* 14(5).

Lambrechts, J.J.N. 1979. Geology, geomorphology and soils. In: Day, J., Siegfried, W.R., Louw, G.N. and Jarman, M.L. (eds). Fynbos ecology: a preliminary synthesis. *South African National Scientific Programmes Report No*. 40. Council for Scientific and Industrial Research, Pretoria, South Africa. 166 pp.

Lamouroux, N. 1998. Depth probability distributions in stream reaches. *Journal of Hydraulic Engineering* 124: 224-227.

Lamouroux, N., Statzner, B., Fuchs, U., Kohmann, F. and Schmedtje, U. 1992. An unconventional approach to modeling spatial and temporal variability of local shear stress in stream segments. *Water Resources Research* 28(12): 3251-3258.

Lamouroux, N., Souchon, Y. and Herouin, E. 1995. Predicting velocity frequency distributions in stream reaches. *Water Resources Research* 31(9): 2367-2375.

Lamouroux, N., Capra, H. and Pouilly, M. 1998. Predicting habitat suitability for lotic fish: linking statistical hydraulic models with multivariate habitat use models. *Regulated Rivers: Research & Management* 14: 1-11.

Lamouroux, N., Olivier, J., Persat, H., Pouilly, M., Souchon, Y. and Statzner, B. 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater Biology* 42: 1-25.

Lamouroux, N. and Souchon, Y. 2002. Simple predictions of instream habitat model outputs for fish habitat guilds in large streams. *Freshwater Biology* 47: 1531-1542.

Lancaster, J. 2000. Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. *Journal of Animal Ecology* 69: 442-457.

Lancaster, J., Hildrew, A.G. and Townsend, C.R. 1990. Stream flow and predation effects on the spatial dynamics of benthic invertebrates. *Hydrobiologia* 203: 177-190.

Lancaster, J. and Hildrew, A.G. 1993a. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* 12(4): 385-393.

Lancaster, J. and Hildrew, A.G. 1993b. Characterizing in-stream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1663-1675.

Lancaster, J. and Belyea, L.R. 1997. Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society* 16(1): 221-238.

Lancaster, J. and Belyea, L.R. 2006. Defining the limits to local density: alternative views of abundance-environment relationships. *Freshwater Biology* 51: 783-796.

Larimore, R.W., Childers, W.F. and Heckrotte, C. 1959. Destruction and re-establishment of stream fish and invertebrates affected by drought. *Transactions of the American Fisheries Society* 88: 261-285.

Layzer, J.B., Nehus, T.J., Pennington, W., Gore, J.A. and Nestler, J.M. 1989. Seasonal variation in the composition of drift below a peaking hydroelectric project. *Regulated Rivers: Research & Management* 3:305-317.

Leathe, S. and Nelson, F.A. 1986. A literature evaluation of Montana's wetted perimeter inflection point method for deriving instream flow recommendations. Technical Report. Montana Department of Fish, Wildlife and Parks, Helena, Montana, U.S.A.

Leclerc, M., Boudreault, A., Bechara, J.A. and Corfa, G. 1995. Two-dimensional hydrodynamic modelling: a neglected tool in the Instream Flow Incremental Methodology. *Transactions of the American Fisheries Society* 124: 645-662.

Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds). 1996. *Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics*. INRS-Eau, Québec, Canada.

Ledger, M. E. and Hildrew, A. G. 2001. Recolonization by the benthos of an acid stream following a drought. *Archiv für Hydrobiologie* 152(1): 1-17.

Leonard, P.M. and Orth, D.J. 1988. Use of habitat guilds to determine instream flow requirements. *North American Journal of Fisheries Management* 8: 399-409.

Leopold, L.B. and Maddock, T.Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. *Geol. Survey Prof. Paper* 252. U.S.G.S., Washington, D.C., U.S.A.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

Levin, S.A., Kimball, K.D., McDowell, W.H. and Kimball, S.H. 1984. New perspectives in ecotoxicology. *Environmental Management* 8: 375-442.

Lillehammer, A. and Saltveit, S.J. (eds). 1984a. *Regulated rivers*. Universitetsforlaget As, Oslo, Norway. 540 pp.

Lillehammer, A. and Saltveit, S.J. 1984b. The effect of the regulation on the aquatic macroinvertebrate fauna of the River Suldalslågen, western Norway. Chapter III: Invertebrates. Pp. 201-210. In: Lillehammer, A. and Saltveit S.J. (eds). *Regulated rivers*. Universitetsforlaget As, Oslo, Norway. 540 pp.

Loar, J.M., Sale, M.J. and Cada, G.F. 1986. Instream flow needs to protect fishery resources. *Water Forum '86: World Water Issues in Evolution*. *Proceedings of ASCE Conference/HY. IR, EE, WR, WW Divs*. Long Beach, California, August 4-6, 1986. California, U.S.A.

Locke, A. 1988. IFIM - microhabitat criteria development: data pooling considerations. Pp 31-54. In: Bovee, K.D. and Zuboy, J.R. (eds). Proceedings of a workshop on the development and evaluation of habitat suitability criteria. *U.S. Fish Wildl. Serv. Biol. Rep.* 88(11). 407 pp.

Logan, P. and Brooker, M.P. 1983. The macroinvertebrate faunas of riffles and pools. *Water Research* 17(3): 263-270.

Low, A.B. and Rebelo, A.G. (eds). 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environment Affairs and Tourism, Pretoria, South Africa.

Lytle, D.H. and Poff, N.L. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19(2): 94-100.

Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 617-628.

Magurran, A.E. 1988. *Ecological diversity and its measurement.* Princeton University Press, New Jersey, U.S.A. 167 pp.

Malan, H.L. and Day, J.A. 2002a. Development of numerical methods for predicting relationships between stream flow, water quality and biotic responses in rivers. *Water Research Commission Report No.* 956/1/02. Water Research Commission, Pretoria, South Africa.

Malan, H.L. and Day, J.A. 2002b. Linking discharge, water quality and biotic response in rivers: a literature review. *Water Research Commission Report No.* 956/2/02. Water Research Commission, Pretoria, South Africa.

Marchant, R. 1988. Seasonal and longitudinal patterns in the macroinvertebrate communities of cobbles from the upper La Trobe River, Victoria, Australia. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1389-1393.

Mathews, R. and Richter, B.D. 2007. Application of the indicators of hydrologic alteration software in environmental flow setting. *Journal of the American Water Resources Association* 43(5): 1-14.

Mathur, D., Bason, W.H., Purdy, E.J.Jr. and Silver, C.A. 1985. A critique of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 825-831.

Matthaei, C.D., Uehlinger, U. and Frutiger, A. 1997. Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology* 37: 61-77.

Matthaei, C.D. and Townsend, C.R. 2000. Long-term effects of local disturbance history on mobile stream invertebrates. *Oecologia* 125: 119-126.

Matthaei, C.D., Arbuckle, C.J. and Townsend, C.R. 2000. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society* 19(1): 82-93.

Matthews, R.C. Jr. and Bao, Y. 1991. The Texas method of preliminary instream flow determination. *Rivers* 2(4): 295-310.

McAuliffe, J.R. 1983. Competition, colonization patterns, and disturbance in stream benthic communities. Pp. 137-155. In: Barnes, J.R. and Minshall, G.W. (eds). *Stream ecology. Application and testing of general ecological theory*. Plenum Press, New York, U.S.A. 399 pp.

McAuliffe, J.R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65(3): 894-908.

McCabe, D.J. and Gotelli, N.J. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* 124: 270-279.

McCafferty, W.P. and Provonsha, A.V. 1981. *Aquatic entomology.* Jones and Bartlett Publishers, Inc., Boston, U.S.A. 448 pp.

McCully, P. 2001. *Silenced rivers: the ecology and politics of large dams. Enlarged and updated edition*. Zed books, London and New York, U.K. and U.S.A. 359 pp.

McElravy, E.P., Lamberti, G.A., and Resh, V.H. 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society* 8(1): 51-63.

McIntosh, M.D., Benbow, M.E. and Burky, A.J. 2002. Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications* 18: 569-581.

McIntosh, M.D., Schmitz, J.A., Benbow, M.E. and Burky, A.J. 2008. Structural and functional changes of tropical riffle macroinvertebrate communities associated with stream flow withdrawal. *River Research and Applications* 24(8): 1045-1055.

McMahon, T. A. and Finlayson, B. L. 2003. Droughts and anti-droughts: the low-flow hydrology of Australian rivers. *Freshwater Biology* 48: 1147-1160.

Meffe, G.K. and Minckley, W.L. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *American Midland Naturalist* 117: 177-191.

Menge, B.A. and Sutherland, J.P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Midland Naturalist* 130: 730-757.

Menge, B.A. and Olson, A.M. 1990. Role of scale and environmental factors in regulation of community structure. *Tree* 5(2): 52-57.

Merritt, R.W. and Cummins, K.W. 1984. *An introduction to the aquatic insects of North America. 2nd. ed.* Kendall/Hunt Publishing Company, Dubuque, Iowa, U.S.A. 722 pp.

Meyerhoff, R.D. and Lind, O.T. 1987. Factors affecting the benthic community structure of a discontinous stream in Guadelupe Mountains National Park, Texas. *Internationale Revue gesamten Hydrobiologie* 72(3): 283-296.

Midgley, D.C., Pitman, W.V. and Middleton, B.J. (compilers). 1994. Surface water resources of South Africa 1990 (WR90). Volume IV: Western Cape. *Water Research Commission Report No.* 298/4.1/94. Water Research Commission, Pretoria, South Africa.

Milhous, R.T., Updike, M.A. and Schneider, D.M. 1989. Physical habitat simulation system reference manual - version 2. *Instream Flow Information Paper* 26. U.S.D.I. Fish Wildl. Serv. Biol. Rep. 89(16).

Millennium Ecosystem Assessment (MA). 2005. *Ecosystem services and human well-being: wetlands and water synthesis.* World Resources Institute, Washington D.C., U.S.A. 68 pp.

Miller, A.M. and Golladay, S.W. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. *Journal of the North American Benthological Society* 15(4): 670-689.

Milner, A. 1994. System recovery. Pp 76-98. In: Calow, P. and Petts, G.E. (eds). *The rivers handbook. Vol. 2*. Blackwell Scientific, Oxford, U.K.

Minshall, G.W. 1984. Aquatic insect-substratum relationships. Pp. 258-400. In: Resh, V.H. and Rosenberg, D.M. (eds). *The ecology of aquatic insects*. Praeger Scientific, New York, U.S.A.

Minshall, G.W. 1988. Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* 7: 263-288.

Minshall, G.W. and Winger, P.V. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* 49: 580-582.

Minshall, G.W. and Minshall, J.N. 1977. Microdistribution of benthic invertebrates in a rocky mountain (U.S.A.) stream. *Hydrobiologia* 55(3): 231-249.

Minshall, G.W. and Petersen, R.C.Jr. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archiv für Hydrobiologie* 104(1): 49-76.

Mitsch, W.J. and Gosselink, J.G. 2000. Wetland hydrology. Chapter 5: 107-153. In: *Wetlands. Third edition*. John Wiley and Sons, Inc., New York, U.S.A. 920 pp.

Modde, T. and Hardy, T.B. 1992. Influence of different microhabitat criteria on salmonid habitat simulation. *Rivers* 3(1): 37-44.

Molden, D. (ed.). 2007. *Water for food, water for life: a comprehensive assessment of water management in agriculture.* Earthscan, London, U.K. and International Water Management Institute, Colombo, Sri Lanka. 643 pp.

Moll, E. and Scott, L. 1981. *Trees and shrubs of the Cape Peninsula*. University of Cape Town, Rondebosch, South Africa. 119 pp.

Monk, W.A., Wood, P.J., Hannah, D.M., Wilson, D.A., Extence, C.A. and Chadd, R.P. 2006. Flow variability and macroinvertebrate community response within riverine systems. *River Research and Applications* 22: 595-615.

Monk, W.A., Wood, P.J., Hannah, D.M. and Wilson, D.A. 2007. Selection of river flow indices for the assessment of hydroecological change. *River Research and Applications* 23: 113-122.

Moon, B.P. and Dardis, G.F. (eds). 1992. *The geomorphology of southern Africa*. Southern Book Publishers Pty Ltd, Halfway House, South Africa. 320 pp.

Moon, H.P. 1956. Observations on a small portion of a drying chalk stream. *Proceedings of the Zoological Society of London* 126(1): 327-333.

Moore, M. 2004. Perceptions and interpretations of environmental flows and implications for future water resource management - a survey study. Unpublished Masters Thesis. Department of Water and Environmental Studies, Linköping University, Sweden. 67 pp.

Morhardt, J.E. 1986. Instream flow methodologies. EA-4819 Research Project 2194-2. Technical Report (Summary). Electric Power Research Institute, California, U.S.A.

Morin, A., Harper, P.P. and Peters, R.H. 1986. Microhabitat preference curves of blackfly larvae (Diptera: Simuliidae): a comparison of three estimation methods. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1235-1241.

Morrison, B.R.S. 1990. Recolonisation of four small streams in central Scotland following drought conditions in 1984. *Hydrobiologia* 208: 261-267.

Mostert, S.A. 1983. Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. *South African Journal of Marine Science* 1: 189-198.

Moyle, P.B. and Baltz, D.M. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. *Transactions of the American Fisheries Society* 114: 695-704.

Moyle, P.B. and Williams, J.E. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. *Conservation Biology* 4(3): 275-284.

Naiman, R.J., Décamps, H., Pastor, J. and Johnston, C.A. 1988. The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* 7: 289-306.

Naiman, R.J. and Turner, M.G. 2000. A future perspective on North America's freshwater ecosystems. *Ecological Applications* 10: 958-970.

Naiman, R.J., Bunn, S.E., Nilsson, C., Petts, G.E., Pinay G., and Thompson L.C. 2002. Legitimizing fluvial ecosystems as users of water: an overview. *Environmental Management* 30: 455-467.

Naiman, R.J., Bunn, S.E., Hiwasaki, L., McClain, M.E., Vörösmarty, C.J. and Zalweski, M. 2006. The science of flow-ecology relationships: clarifying key terms and concepts. White Paper. ESSP Open Science Conference. November 2006. Beijing, China.

Nakamura, S. 1999. Recent river ecosystem conservation efforts downstream of power dams in a densely populated and highly industrialized country: Japan. Keynote speech. International Energy Agency, Annex III – Hydropower and environment. Technical Seminar Report. Madrid, Spain. 19 pp.

Nathan, R.J. and McMahon, T.A. 1990a. Evaluation of automated techniques for base flow and recession analyses. *Water Resources Research* 26: 1465-1473.

Nathan, R.J. and McMahon, T.A. 1990b. Identification of homogenous regions for the purposes of regionalisation. *Journal of Hydrology* 121: 217-238.

Nehring, R.B. and Anderson, R.M. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation System. *Rivers* 4(1): 1-19.

Nelson, F.A. 1980. Evaluation of selected instream flow methods in Montana. Pp. 412-432. In: *Proceedings of the Annual Conference of the Western Association of Fish and Wildlife Agencies*. Montana, U.S.A.

Nestler, J.M., Milhous, R.T. and Layzer, J.B. 1989. Instream habitat modeling techniques. Pp. 295-315. In: Gore, J.A. and Petts, G.E. (eds). *Alternatives in regulated river management*. CRC Press, Inc., Florida, U.S.A.

Nestler, J.M, Schneider L.T, Latka, D and Johnson, P. 1996. Impact analysis and restoration planning using the riverine community habitat assessment and restoration concept (RCHARC). In: Leclerc, M., Capra,. H., Valentin, S., Boudreault, A. and Côté, Y. (eds). *Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics.* INRS-Eau, Québec, Canada.

Newbury, R.W. 1984. Hydrologic determinants of aquatic insect habitats. Pp. 323-357. In: Resh, V.H. and Rosenburg, D.M. (eds). *The ecology of aquatic insects*. Praeger, New York, U.S.A.

Newcombe, C. 1981. A procedure to estimate changes in fish populations caused by changes in stream discharge. *Transactions of the American Fisheries Society* 110: 382-390.

Newson, M.D., Harper, D.M., Padmore, C.L., Kemp, J.L. and Vogel, B. 1998. A cost-effective approach for linking habitats, flow types and species requirements. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8: 431-446.

Newson, M.D. and Newson, C.L. 2000. Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progress in Physical Geography* 24(2): 195-217.

Niemi, G.J., Devore, P., Detenbeck, N., Taylor, D., Lima, A. Pastor, J., Yount, J.D. and Naiman, R.J. 1990. Overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management* 14(5): 571-587.

Niemi, G.J., Detenbeck, N.E. and Perry, J.A. 1993. Comparative analysis of variables to measure recovery rates in streams. *Environmental Toxicology and Chemistry*. 12: 1541-1547.

Nilsson, C. and Berggren, K. 2000. Alterations of riparian ecosystems caused by river regulation. *BioScience* 50: 783-792.

Nilsson, C., Reidy C.A., Dynesius, M. and Revenga, C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308: 405-408.

Nilsson, C. and Renöfält, B.M. 2008. Linking flow regime and water quality for rivers: a challenge to adaptive catchment management. *Ecology and Society* 13(2): 18.

Noble, R.G. and Hemens, J. 1978. Inland water ecosystems in South Africa - a review of research needs. *S. Afr. Nat. Sci. Prog. Rep. No.* 34. Council for Scientific and Industrial Research, Pretoria, South Africa. 150 pp.

Norwegian Institute of Technology. 1994. *Proceedings of the first international symposium on habitat hydraulics*. Trondheim, Norway.

Nowell, A.R.M. and Jumars, P.A. 1984. Flow environments of aquatic benthos. *Annual Review of Ecology, Evolution, and Systematics* 15: 303-328.

O'Keeffe, J.H. 1995. Managing rivers and their water resources as sustainable ecosystems: the South African experience. In: Harper, D.M. and Ferguson, A.J.D. (eds). *The ecological basis for river management*. John Wiley and Sons, Chichester, U.K.

O'Keeffe, J.H. 2000. Environmental flow assessments within the South Africa integrated planning process for water resources. Chpt. 4: 41-52. In: King, J.M., Tharme, R.E. and De Villiers, M.S. (eds). Environmental flow assessments for rivers: manual for the Building Block Methodology. *Water Research Commission Technology Transfer Report No.* TT131/00. Water Research Commission, Pretoria, South Africa. 340 pp.

O'Keeffe, J.H., Danilewitz, D.B. and Bradshaw, J.A. 1987. An expert system approach to the assessment of the conservation status of rivers. *Biological Conservation* 40: 69-84.

O'Keeffe, J.H., Davies, B.R., King, J.M. and Skelton, P.H. 1989a. The conservation status of southern African rivers. In: Huntley, B.J. (ed.). *Biotic Diversity in Southern Africa.* Oxford University Press, Cape Town, South Africa. 380 pp.

O'Keeffe, J.H., King, J.M., Day, J.A., Rossouw, O., Van Der Zel, D.W. and Skoroszewski, R. 1989b. General concepts and approaches to instream flow assessment. In: Ferrar, A.A. (ed.). Ecological flow requirements for South African rivers. *S. Afr. Nat. Sci. Prog. Rep. No*. 162. Council for Scientific and Industrial Research, Pretoria, South Africa.

O'Keeffe, J.H. and Davies, B.R. 1991. Conservation and management of the rivers of the Kruger National Park: suggested methods for calculating instream flow needs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 1: 55-71.

O'Keeffe, J.H., Weeks, D.C. Fourie, A. and Davies, B.R. 1996. A pre-impoundment study of the Sabie-Sand river system, Mpumalanga with special reference to predicted impacts on the Kruger National Park. Volume 3. The effects of proposed impoundments and management recommendations. *Water Research Commission Report No.* 294/3/96. Water Research Commission, Pretoria, South Africa. 111 pp.

O'Keeffe, J.H. and Uys, M. 1998. Invertebrate diversity in natural and modified perennial and temporary flow regimes. Section 2: Chapter 13. In: McComb, A.J. and Davis, J.A. (eds). *Wetlands for the future*. Gleneagles Publishing, Adelaide, Australia.

O'Keeffe, J. and Dickens, C. 2000. Aquatic invertebrates. Chpt. 17: 231-244. In: King, J.M., Tharme, R.E. and De Villiers, M.S. (eds). Environmental flow assessments for rivers: manual for the Building Block Methodology. *Water Research Commission Technology Transfer Report No.* TT131/00. Water Research Commission, Pretoria, South Africa. 340 pp.

O'Keeffe, J., Hughes, D. and Tharme, R. 2002. Linking ecological responses to altered flows, for use in environmental flow assessments: the Flow Stressor-Response method. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 28: 84-92.

Olden, J.D. and Poff, N.L. 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications* 19: 101-121.

O'Neil, M.P. and Abrahams, A.D. 1984. Objective identification of pools and riffles. *Water Resources Research* 20(7): 921-926.

Ormerod, S.J. and Edwards, R.W. 1987. The ordination and classification of macroinvertebrate assemblages in the catchment of the River Wye in relation to environmental factors. *Freshwater Biology* 17: 533-546.

Orth, D.J. 1987. Ecological considerations in the development and application of instream flow-habitat models. *Regulated Rivers: Research & Management* 1: 171-181.

Orth, D.J. and Maughan, O.E. 1982. Evaluation of the Incremental Methodology for recommending instream flows for fishes. *Transactions of the American Fisheries Society* 111: 413-445.

Orth, D.J. and Maughan, O.E. 1983. Microhabitat preferences of benthic fauna in a woodland stream. *Hydrobiologia* 106: 157-168.

Orth, D.J. and Leonard, P.M. 1990. Comparison of discharge methods and habitat optimization for recommending instream flows to protect fish habitat. *Regulated Rivers: Research & Management* 5: 129-138.

Osenberg, C.W., Schmitt, R.J., Holbrook, S.J., Abu-Saba, K.E. and Flegal, A.R. 1994. Detection of environmental impacts: natural variability, effect size, and power analysis. *Ecological Applications* 4(1): 16-30.

O'Shea, D.T. 1995. Estimating minimum instream flow requirements for Minnesota streams from hydrologic data and watershed characteristics. *North American Journal of Fisheries Management* 15: 569-578.

Padmore, C.L. 1997. Physical biotopes in representative river channels: identification, hydraulic characterisation and application. Unpublished Ph.D. Thesis. Department of Geography, University of Newcastle. 237 pp.

Padmore, C.L. 1998. The role of physical biotopes in determining the conservation status and flow requirements of British rivers. *Aquatic Ecosystem Health and Management* 1: 25-35.

Padmore, C.L., Newson, M.D. and Charlton, M.E. 1998. Instream habitat in gravel bed rivers: identification and characterisation of biotopes. Pp. 345-364. In: Klingeman, P.C., Beschta, R.L., Komar, P.D. and Bradley, J.B. (eds). *Gravel bed rivers in the environment*. Water Resources Publications, Highlands Ranch, CO, U.S.A.

Palau, A. and Alcazar, J. 1996. The basic flow: an alternative approach to calculate minimum environmental instream flows. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds). *Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics*. Québec, June 1996. Volume B. INRS-Eau, Québec, Canada.

Palmer, C.G. 1999. The application of ecological research in the development of a new water law in South Africa. *Journal of the North American Benthological Society* 18: 132-142.

Palmer, C.G., O'Keeffe, J.H. and Palmer, A.R. 1991. Are macroinvertebrate assemblages in the Buffalo River, southern Africa, associated with particular biotopes? *Journal of the North American Benthological Society* 10: 349-357.

Palmer C.G. and Scherman, P.-A. 1999. Application of an artificial stream system to investigate the water quality tolerances of indigenous, South African riverine macroinvertebrates. *Water Research Commission Report No.* 686. Water Research Commission, Pretoria, South Africa.

Palmer, M.A., Bely, A.E. and Berg, K.E. 1992. Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia* 89: 182-194.

Palmer, M.A. and Poff, N.L. 1997. Heterogeneity in streams: the influence of environmental heterogeneity on patterns and processes in streams. *Journal of the North American Benthological Society* 16(1): 169-173.

Palmer, M.A., Hakenkamp, C.C. and Nelson-Baker, K. 1997. Ecological heterogeneity in streams: why variance matters. *Journal of the North American Benthological Society* 16(1): 189-202.

Palmer, M.A., Swan, C.M., Nelson, K., Silver, P. and Alvestad, R. 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecology* 15: 563-576.

Parasiewicz, P. and Dunbar, M.J. 2001. Physical habitat modeling for fish - a developing approach. *Archiv für Hydrobiologie Supplement* 135(2-4): 1-30.

Pardo, I. and Armitage, P.D. 1997. Species assemblages as descriptors of mesohabitats. *Hydrobiologia* 344: 111-128.

Parsons, M., Thoms, M.C. and Norris, R.H. 2004. Using hierarchy to select scales of measurement in multiscale studies of stream macroinvertebrate assemblages. *Journal of the North American Benthological Society* 23(2): 157-170.

Paxton, B.R. 2000. Microhabitat suitability curves derived for the mayfly larvae (Ephemeroptera) of a south-western Cape foothill river. Unpublished Honours Thesis. University of Cape Town, Rondebosch, Cape Town, South Africa. 36 pp.

Pearson, W.D. and Franklin, D.R. 1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. *Ecology* 49: 75-81.

Peckarsky, B.L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pp. 303-323. In: Fontaine, T.D. III and Bartell, S.M. (eds). *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers, Ann Arbor, Michigan, U.S.A. 494 pp.

Peckarsky, B.L., Cooper, S.D. and McIntosh, R. 1997. Extrapolating from individual behaviour to populations and communities in streams. *Journal of the North American Benthological Society* 16(2): 375-390.

Perry, S.A. and Perry, W.B. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia* 134: 171-182.

Peterson, C.G. and Stevenson, R.J. 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73(4): 1445-1461.

Petts, G.E. 1979. Complex response of river channel morphology subsequent to reservoir construction. *Progress in Physical Geography* 3: 329-362.

Petts, G.E. 1980. Long term consequences of upstream impoundment. *Environmental Conservation* 7(4): 325-332.

Petts, G.E. (ed.) 1984a. *Impounded rivers: perspectives for ecological management*. John Wiley and Sons, Chichester, U.K. 326 pp.

Petts, G.E. 1984b. Channel morphology. In: Petts, G.E. (ed.). *Impounded rivers: perspectives for ecological management*. John Wiley and Sons, Chichester, U.K. 326 pp.

Petts, G.E. 1987. Time-scales for ecological changes. Pp. 257-266. In: Craig, J.F. and Kemper, J.B. (eds). *Regulated streams: advances in ecology*. Plenum Press, New York, U.S.A.

Petts, G.E. 1989. Perspectives for ecological management of regulated rivers. Pp. 3-24. In: Gore, J.A. and Petts, G.E. (eds). *Alternatives in regulated river management*. CRC Press, Inc., Florida, U.S.A.

Petts, G.E. 1996. Water allocation to protect river ecosystems. *Regulated Rivers: Research & Management* 12: 353-365.

Petts, G.E. and Bickerton, M.A. 1994. The River Babingley: a study of in-river needs. Report to the National Rivers Authority, Anglian Region. Peterborough, U.K.

Petts, G.E and Maddock, I. 1994. Flow allocation for in-river needs. Pp. 60-79. In: Petts, G.E. and Calow, P. (eds). *River restoration.* Blackwell Science, Oxford, U.K.

Petts, G., Maddock, I., Bickerton, M. and Ferguson, A.J.D. 1995. Linking hydrology and ecology: the scientific basis for river management. Chapter 1: 1-16. In: Harper, D.M. and Ferguson, A.J.D. (eds). *The ecological basis for river management*. John Wiley and Sons, Chichester, U.K.

Petts, G.E., Crawford, C. and Clarke, R. 1996. Determination of minimum flows. *Environment Agency R and D Note* 449. Environmental Research and Management, University of Birmingham, Bristol, Britain.

Petts, G.E., Bickerton, M.A., Crawford, C., Lerner, D.N. and Evans, D. 1999. Flow management to sustain groundwater-dominated stream ecosystems. *Hydrological Processes* 13: 497-513.

Phélines, R.F., Coke, M. and Nicol, S.M. 1973. Some biological consequences of the damming of the Pongola River. *Proceedings of the Onzième Congrès des Grands Barrages.* Q.40 - R.14. Madrid, Spain.

Picker, M.D. and Samways, M.J. 1996. Faunal diversity and endemicity of the Cape Peninsula, South Africa - a first assessment. *Biodiversity and Conservation* 5: 591-606.

Picker, M., Griffiths, C. and Weaving, A. 2004. *Field guide to insects of South Africa*. *New Edition*. Struik Publishers, Cape Town, South Africa. 444 pp.

Pickett, S.T.A. and White, P.S. 1985. Patch dynamics: a synthesis. Pp. 371-384. In: Pickett, S.T.A. and White, P.S. (eds). *The ecology of natural disturbance and patch dynamics*. Academic Press, Inc., Orlando, U.S.A. 472 pp.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. and Collins, S.L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54: 129-136.

Pires, A.M., Cowx, I.G. and Coelho, M.M. 2000. Benthic macroinvertebrate communities of intermittent streams in the middle of the Guadiana Basin (Portugal). *Hydrobiologia* 435: 167-175.

Poff, N.L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* 11(1): 86-92.

Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* 36: 71-91.

Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16(2): 391-409.

Poff, N.L. and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1805-1818.

Poff, N.L. and Ward, J.V. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14: 629-645.

Poff, N.L. and Ward, J.V. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1926-1936.

Poff, N.L. and Allan, J.D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76(2): 606-627.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E. and Stromberg, J.C. 1997. The natural flow regime. A paradigm for river conservation and restoration. *BioScience* 47: 769-784.

Poff, N.L., Allan, J.D., Palmer, M.A., Hart, D.D., Richter, B.D., Arthington, A.H., Rogers, K.H., Meyer, J.L. and Stanford, J.A. 2003. River flows and water wars: emerging science for environmental decision making. *Frontiers in Ecology and the Environment* 1(6): 298-306.

Poff, N.L., Olden, J.D., Pepin, D.M. and Bledsoe, B.P. 2006a. Placing global stream flow variability in geographic and geomorphic contexts. *River Research and Applications* 22: 149-166.

Poff, N.L., Bledsoe, B.P. and Cuhaciyan, C.O. 2006b. Hydrologic variation with land use across the contiguous United States: geomorphic and ecological consequences for stream ecosystems. *Geomorphology* 79: 264–285.

Poff, N.L., Richter, B.D., Arthington, A.H., Bunn, S.E., Naiman, R.J., Kendy, E., Acreman, M., Apse, C., Bledsoe, B.P., Freeman, M.C., Henriksen, J., Jacobson, R.B., Kennen, J.G., Merritt, D.M., O'Keeffe, J.H., Olden, J.D., Rogers, K., Tharme, R.E. and Warner, A. 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology* 55: 147-170.

Pollard, S.R., Weeks, D.C. and Fourie, A. 1996. A pre-impoundment study of the Sabie-Sand River system, Mpumalanga with special reference to predicted impacts on the Kruger National Park. Volume Two. Effects of the 1992 drought on the fish and macro-invertebrate fauna. *Water Research Commission Report No*. 294/2/96. Water Research Commission, Pretoria, South Africa. 101 pp.

Postel, S. 1995. Where have all the rivers gone? *World Watch* 8: 9-19.

Postel, S.L. 1998. Water for food production: will there be enough in 2025? *BioScience* 48: 629-637.

Postel, S.L, Daily, G.C. and Ehrlich PR. 1996. Human appropriation of renewable fresh water. *Science* 271: 785-788.

Postel, S. and Richter, B. 2003. *Rivers for life: managing water for people and nature.* Island Press, Washington D.C., U.S.A. 253 pp.

Powell, G.L., Matsumoto, J. and Brock, D.A. 2002. Methods for determining minimum freshwater inflow needs of Texas bays and estuaries. *Estuaries* 25(6B): 1262-1274.

Power, M.E., Stout, R.J., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Statzner, B. and Wais De Badgen, I.R. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7: 456-479.

Power, M.E., Dietrich, W.E. and Finlay, J.C. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental Management* 20(6): 887-895.

Prewitt, C.G. and Carlson, C.A. 1980. Evaluation of four instream flow methodologies used on the Yampa and White Rivers, Colorado. Biological Sciences Series Number Two. Bureau of Land Management. Denver, Colorado, U.S.A. 65 pp.

Pridmore, R.D. and Roper, D.S. 1985. Comparison of the macroinvertebrate faunas of runs and riffles in three New Zealand streams. *New Zealand Journal of Marine and Freshwater Research* 19: 283-291.

Pringle, C.M. 1997. Exploring how disturbance is transmitted upstream: going against the flow. *Journal of the North American Benthological Society* 16: 425-438.

Pringle, C.M. 2000. River conservation in tropical versus temperate latitudes. Chapter 15: 371-384. In: Boon, P.J., Davies, B.R. and Petts, G.E. *Global perspectives on river conservation: science, policy and practice.* John Wiley and Sons Ltd., Chichester, U.K. 517 pp.

Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L. and Winterbourn, M.J. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society* 7: 503-524.

Pringle, C.M., Freeman, M.C. and Freeman, B.J. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. *BioScience* 50(9): 807-823.

Puckridge, J.T., Sheldon, F., Walker, K.F. and Boulton, A.J. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* 49: 55-72.

Pusey, B.J. 1998. Methods addressing the flow requirements of fish. Pp. 66-105. In: Arthington, A.H., and Zalucki, J.M. (eds). Comparative evaluation of environmental flow assessment techniques: review of methods. *Land and Water Resources Research and Development Corporation Occasional Paper No*. 27/98. Canberra, Australia.

Pyrce, R. 2004. Hydrological low flow indices and their uses. Comparative evaluation of environmental flow assessment techniques: review of methods. *Watershed Science Centre Report No*. 04-2004. Ontario, Canada. 33 pp.

Quinn, J.M. and Hickey, C.W. 1994. Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. *Freshwater Biology* 32: 489-500.

Ractliffe, S.G. and Brown, C.A. 1994. Molenaars River, south-western Cape: situation assessment of the riverine ecosystem. Final Report. Commissioned by Ninham Shand Consulting Engineers, Cape Town. Southern Waters Ecological Research and Consulting cc, University of Cape Town, South Africa. 71 pp.

Ractliffe, S.G., Snaddon, C.D. and Brown, C.A. 1996. The Riviersonderend: situation assessment, with specific reference to the effects of Theewaterskloof Dam on the riverine ecosystem. Report to the Department of Water Affairs and Forestry. Southern Waters Ecological Research and Consulting cc, University of Cape Town, South Africa. 162 pp.

Rader, R.B. and Ward, J.V. 1989. The influence of environmental predictability characteristics on the structure of a guild of mountain stream insects. *Oikos* 54: 107-116.

Rader, R.B. and Belish, T.A. 1999. Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research & Management* 15: 353-363.

Radford, D.W. and Hartland-Rowe, R. 1971. A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. *Journal of Applied Ecology* 8: 883-903.

Reice, S.R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* 67: 90-97.

Reice, S.R., Wissmar, R.C. and Naiman, R.J. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management* 14(5): 647-659.

Reiser, D.W., Ramsey, M.P. and Lambert, T.R. 1987. Considerations in assessing flushing flow needs in regulated stream systems. Pp. 45-57. In: Craig, J.F. and Kemper, J.B. (eds). *Regulated streams: advances in ecology*. Plenum Press, New York.

Reiser, D.W., Ramey, M.P. and Wesche, T.A. 1989a. Flushing flows. In: Gore, J.A. and Petts, G.E. (eds). *Alternatives in regulated river management*. CRC Press, Inc., Florida, U.S.A.

Reiser, D.W., Wesche, T.A. and Estes, C. 1989b. Status of instream flow legislation and practise in North America. *Fisheries* 14(2): 22-29.

Rempel, L.L., Richardson, J.S. and Healey, M.C. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology* 45: 57-73.

Resh, V.H. 1982. Age structure alteration in a caddisfly population after habitat loss and recovery. *Oikos* 38: 280-284.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B. and Wissmar, R.C. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7(4): 433-455.

Resh, V.H., Hildrew, A.G., Statzner, B. and Townsend, C.R. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biology* 31: 539-554.

Revenga, C., Murray, S., Abramowitz, J. and Hammond, A. 1998. *Watersheds of the world: ecological value and vulnerability*. World Resources Institute and Worldwatch Institute, Washington, D.C., U.S.A.

Revenga, C., Brunner, J., Henninger N., Kassem, K. and Payne, R. 2000. *Pilot analysis of global ecosystems: freshwater ecosystems*. World Resources Institute, Washington, D.C., U.S.A. 83 pp.

Revenga, C. and Kura, Y. 2003. Status and trends of biodiversity of inland water ecosystems. *Technical Series No*. 11. Secretariat of the Convention on Biological Diversity, Montreal, Canada. 116 pp.

Ricciardi, A. and Rasmussen, J.B. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13: 220-222.

Richards, R.P. 1990. Measures of flow variability and a new flow-based classification of Great Lakes tributaries. *Journal of Great Lakes Research* 16: 53-70.

Richardson, B.A. 1986. Evaluation of instream flow methodologies for freshwater fish in New South Wales. Pp. 143-167. In: Campbell, I.C. (ed.). *Stream protection: the management of rivers for instream uses*. Water Studies Centre: Chisholm Institute of Technology, Australia. 249 pp.

Richter, B.D., Baumgartner, J.V., Powell, J. and Braun, D.P. 1996. A method for assessing hydrological alteration within ecosystems. *Conservation Biology* 10(4): 1163-1174.

Richter, B.D., Baumgartner, J.V., Wigington, R. and Braun, D.P. 1997a. How much water does a river need? *Freshwater Biology* 37: 231-249.

Richter, B.D., Braun, D.P., Mendelson, M.A. and Master, L.L. 1997b. Threats to imperiled freshwater fauna. *Conservation Biology* 11(5): 1081-1093.

Richter, B.D., Mathews, R., Harrison, D.L. and Wigington, R. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications* 13(1): 206-224.

Richter, B.D., Warner, A.T., Meyer, J.L. and Lutz, K. 2006. A collaborative and adaptive process for developing environmental flow recommendations. *River Research and Applications* 22: 297-318.

Rijsberman, F.R. (ed.). 2000. *World water scenarios: analyses*. Earthscan, London, U.K.

Riseng, C.M., Wiley, M.J. and Stevenson, R.J. 2004. Hydrologic disturbance and nutrient effects on benthic community structure in midwestern US streams: a covariance structure analysis. *Journal of the North American Benthological Society* 23(2): 309-326.

Roberts, C.P.R. 1983. Environmental constraints on water resources development. *Proceedings of the South African Institution of Civil Engineers* 1: 16-23.

Robson, B.J. 1996. Small spate disturbance and the complexity of habitat architecture in Mountain River, Tasmania. *Marine and Freshwater Research* 47: 851-855.

Robson, B.J. and Barmuta, L.A. 1998. The effect of two scales of habitat architecture on benthic grazing in a river. *Freshwater Biology* 39: 207-220.

Robson, B.J., Chester, E.T. and Davis, J.A. 1999. Manipulating the intensity of near-bed turbulence in rivers: effects on benthic invertebrates. *Freshwater Biology* 42: 645-653.

Rogers, K.H. 2006. The real river management challenge: integrating scientists, stakeholders and service agencies. *River Research and Applications* 22: 269-280.

Rosegrant, M.W. and Cai, X. 2002. Global water demand and supply projections. Part 2. Results and prospects to 2025. *Water International* 27(2): 170-182.

Rosenberg, D.M., Berkes, F., Bodaly, R.A., Hecky, R.E., Kelly, C.A. and Rudd, J.W.M. 1997. Large-scale impacts of hydroelectric development. *Environmental Reviews* 5: 27-54.

Rosenberg, D.M., McCully, P. and Pringle, C.M. 2000. Global-scale environmental effects of hydrological alterations: introduction. *BioScience* 50(9): 746-751.

Rosgen, D.L. 1994. A classification of natural rivers. *Catena* 22: 169-199.

Rowntree, K. M. (ed.). 1996. The hydraulics of physical biotopes – terminology, inventory and calibration. Workshop Report. Citrusdal, 4-7 February 1995. *Water Research Commission Report* KV84/96. Water Research Commission, Pretoria, South Africa. 51 pp.

Rowntree, K. M. 2000. Geomorphology. Chpt. 14: 169-194. In: King, J.M., Tharme, R.E. and De Villiers, M.S. (eds). Environmental flow assessments for rivers: manual for the Building Block Methodology. *Water Research Commission Technology Transfer Report No.* TT131/00. Water Research Commission, Pretoria, South Africa. 340 pp.

Rowntree, K.M. and Wadeson, R.A. 1996. Translating channel morphology into hydraulic habitat: application of the hydraulic biotope concept to an assessment of discharge related habitat changes. In: Leclerc, M., Capra, H., Valentin, S., Boudreault, A. and Côté, Y. (eds). *Ecohydraulics 2000. Proceedings of the 2nd International Symposium on Habitat Hydraulics*. Québec, June 1996. Volume B. INRS-Eau, Québec, Canada.

Rowntree, K.M. and Wadeson, R.A. 1997. A hierarchical geomorphological model for the assessment of instream flow requirements. *Geoöko plus* 4: 85-100.

Rowntree, K and Wadeson, R. 1998. A geomorphological framework for the assessment of instream flow requirements. *Aquatic Ecosystem Health and Management* 1: 125-141.

Rowntree, K.M. and Wadeson, R.A. 1999. A hierarchical geomorphological model for the classification of selected South African river systems. *Water Research Commission Final Report*. Water Research Commission, Pretoria, South Africa. 334 pp.

Ruse, L. and Davison, M. 2000. Long-term data assessment of chironomid taxa structure and function in the River Thames. *Regulated Rivers: Research & Management* 16: 113-126.

Saltveit, S.J., Brittain, J.E. and Lillehammer, A. 1987. Stoneflies and river regulation - a review. Pp. 117-129. In: Craig, J.F. and Kemper, J.B (eds). *Regulated streams: advances in ecology*. Plenum Press, New York and London, U.S.A. and U.K.

Scarsbrook, M.R. and Townsend, C.R. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology* 29: 395-410.

Scherman, P.-A., Muller, W.J. and Palmer, C.G. 2003. Links between ecotoxicology, biomonitoring and water chemistry in the integration of water quality into environmental flow assessments. *River Research and Applications* 19: 483-493.

Schindler, D.W. 1987. Detecting ecosystem responses to anthropogenic stress. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 6-25.

Schofield, N., Burt, A. and Connell D. 2003. Environmental water allocation: principles, policies and practices. *Land and Water Australia Technical Report*. Land and Water Australia, Canberra A.C.T., Australia. 38 pp.

Scholtz, C.H. and Holm, E. (eds). 1985. *Insects of southern Africa*. Butterworths Publishers (Pty) Ltd., South Africa. 502 pp.

Scott, D. and Shirvell, C.S. 1987. A critique of the instream flow incremental methodology and observations on flow determination in New Zealand. Pp. 27-43. In: Craig, J.F and Kemper, J.B. (eds). *Regulated streams: advances in ecology*. Plenum Press, New York and London, U.S.A. and U.K.

Scott, K.M.F. 1983. On the Hydropsychidae (Trichoptera) of southern Africa with keys to African genera of imagos, larvae and pupae and species lists. *Annals of the Cape Provincial Museums (Natural History)* 14(8).

Scrimgeour, G.J, Davidson RJ and Davidson, JM. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 22: 337-344.

Scrimgeour, G.J. and Winterbourn, M.J. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* 171: 33-44.

Scullion, J. and Sinton, A. 1983. Effects of artificial freshets on substratum composition, benthic invertebrate fauna and invertebrate drift in two impounded rivers in mid-Wales. *Hydrobiologia* 107: 261-269.

Sedell, J.R, Reeves, G.H., Hauer, F.R., Stanford, J.A and Hawkins, C.P. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* 14: 711-724.

Sheldon, A.L. and Haick, R.A. 1981. Habitat selection and association of stream insects: a multivariate analysis. *Freshwater Biology* 11: 395-403.

Shiklomanov, I.A. 1997. Assessment of water resources and water availability in the world. Comprehensive assessment of the freshwater resources of the world. Technical Report. Stockholm Environment Institute, Stockholm, Sweden.

Shiklomanov, I.A. 2000a. Appraisal and assessment of world water resources. *Water International* 25(1): 11-32.

Shiklomanov, I.A. 2000b. World water resources and water use: present assessment and outlook for 2025. Pp: 160-203. In: Rijsberman, F.R. (ed.). *World water scenarios*. Earthscan, London, U.K.

Shirvell, C.S. 1986. Pitfalls of physical habitat simulation in the instream flow incremental methodology. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1460. 68 pp.

Silver, P., Wooster, D. and Palmer, M.A. 2004. Chironomid responses to spatially structured, dynamic, streambed landscapes. *Journal of the North American Benthological Society* 23(1): 69-77.

Singh, K.P. and Broeren, S.M. 1989. Hydraulic geometry of streams and stream habitat assessment. *Journal of Water Resources Planning and Management* 115(5): 583-597.

Skelton, P.H. 1987. South African Red Data Book - Fish. *South African National Scientific Programmes Report No. 137*. Council for Scientific and Industrial Research, Pretoria, South Africa. 199 pp.

Skelton, P.H. 1993. *A complete guide to the freshwater fishes of southern Africa*. Southern Book Publishers, South Africa. 388 pp.

Slauson, W.L. 1988. Constructing suitability curves from data. Pp. 225-258. In: Bovee, K.D. and Zuboy, J.R. (eds). Proceedings of a workshop on the development and evaluation of habitat suitability criteria. *U.S. Fish Wildl. Serv. Biol. Rep.* 88(11).

Smakhtin, V.U. 2001. Low flow hydrology: a review. *Journal of Hydrology* 240: 147-186.

Smakhtin, V.U., Watkins, D.A. and Hughes, D.A. 1995. Preliminary analysis of low-flow characteristics of South African rivers. *Water SA* 21: 201-210.

Smakhtin, V.U. and Watkins, D.A. 1997. Low-flow estimation in South Africa. *Water Research Commission Report No*. 494/1/97. Pretoria, South Africa.

Smakhtin, V. and Toulouse, M. 1998. Relationships between low-flow characteristics of South African streams. *Water SA* 24(2): 107-112.

Smakhtin, V., Watkins, D.A., Hughes, D.A., Sami, K. and Smakhtina, O.Y. 1998. Methods of catchment-wide assessment of daily low-flow regimes in South Africa. *Water SA* 24(3): 173-185.

Smakhtin, V., Revenga, C. and Döll, P. 2004. A pilot global assessment of environmental water requirements and scarcity. *Water International* 29(3): 307-317.

Smola, N., Vrhovšek, D. and Kosi, G. 1998. Effects of low flow on periphyton in three different types of streams in Slovenia. Pp. 107-116. In: Bretschko, G. and Helešic, J. (eds). *Advances in river bottom ecology*. Backhuys Publishers, Leiden, The Netherlands.

Snaddon, C.D. and Davies, B.R. 1998. A preliminary assessment of the effects of a small South African inter-basin water transfer on discharge and invertebrate community structure. *Regulated Rivers: Research & Management* 14: 421-441.

Snaddon, C.D. and Davies, B.R. 1999. An assessment of the ecological effects of inter-basin water transfer schemes (IBTs) in dryland environments. *Water Research Commission Report No.* 665/1/00. Water Research Commission, Pretoria, South Africa. 83 pp.

Snaddon, C.D, Davies, B.R and Wishart, M.J. 1999. A global overview of inter-basin water transfer schemes, with an appraisal of their ecological, socio-economic and socio-political implications, and recommendations for their management. *Water Research Commission Technology Transfer Report* TT 120/00. Water Research Commission, Pretoria, South Africa. 113 pp.

Sousa, W.P. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. *Oecologia (Berlin)* 45: 72-81.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology, Evolution, and Systematics* 15: 353-391.

South African National Water Act No. 36 of 1998. *Government Gazette Volume* 398*, No.* 19182. 26 August 1998. Cape Town, South Africa.

Southwood, T.R.E. 1988. Tactics, strategies and templates. *Oikos* 52: 3-18.

Sparks, R.E. 1995. Need for ecosystem management of large rivers and their floodplains. *BioScience* 45: 168/9-182.

Specht, R.L. and Moll, E.J. 1983. Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. Pp. 41-65. In: Kruger, F.J., Mitchell, D.T. and Jarvis, J.U.M. (eds). *Mediterranean-type ecosystems. The role of nutrients.* Ecological Studies 43. Springer-Verlag, Berlin. 552 pp.

Stalnaker, C.B. 1979. The use of habitat stucture preferenda for establishing flow regimes necessary for maintenance of fish habitat. Pp. 321-337. In: Ward, J.V. and Stanford, J.A. (eds). *The ecology of regulated streams*. Plenum Press, New York and London, U.S.A. and U.K.

Stalnaker, C.B. 1982. Instream flow assessments come of age in the decade of the 1970s. Pp. 119-142. In: Mason, W.T. and Iker, S. (eds). *Research on fish and wildlife habitat*. EPA-600/8-82-022. Office of Research and Development. U.S. Environmental Protection Agency. Washington, D.C., U.S.A.

Stalnaker, C.B. 1998. The Instream Flow Incremental Methodology. Pp. 9-11. In: Blažková, Š., Stalnaker, C. and Novický, O. (eds). *Hydroecological modelling. Research, practice, legislation and decision-making*. Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Stalnaker, C.B. and Arnette, S.C. 1976. Methodologies for the determination of stream resource flow requirements: an assessment. U.S. Fish and Wildlife Services, Office of Biological Services Western Water Association. 199 pp.

Stalnaker, C.B., Milhous, R.T. and Bovee, K.D. 1989. Hydrology and hydraulics applied to fishery management in large rivers. In: Dodge, D.P. (ed.). Proceedings of the International Large River Symposium. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106: 13-30.

Stalnaker, C.B., Lamb, B.L., Henriksen, J., Bovee, K.D. and Bartholow, J. 1994. *The Instream Flow Incremental Methodology: a primer for IFIM.* National Ecology Research Center, Internal Publication. National Biological Survey. Fort Collins, Colorado, U.S.A. 99 pp.

Stanford, J.A. and Ward, J.V. 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. Pp. 265-278. In: Barnes, J.R. and Minshall, G.W. (eds). *Stream ecology. Application and testing of general ecological theory*. Plenum Press, New York, U.S.A. 399 pp.

Stanford, J.A., Ward, J.V., Liss, W.J., Frissell, C.A., Williams, R.N., Lichatowich, J.A. and Coutant, C.C. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research & Management* 12: 391-413.

Stanley, E.H. and Fisher, S.G. 1992. Intermittency, disturbance, and stability in stream ecosystems. Pp. 271-280. In: Robarts, R.D. and Bothwell, M.L. (eds). *Aquatic ecosystems in semi-arid regions: implications for resource management*. N.H.R.I. Symposium Series 7, Environment Canada, Saskatoon, Canada.

Stanley, E.H., Buschman, D.L., Boulton, A.J., Grimm, N.B. and Fisher, S.G. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist* 131: 288-300.

Stanley, E.H., Fisher, S.G. and Grimm, N.B. 1997. Ecosystem expansion and contraction in streams. *BioScience* 47: 427-435.

StatSoft. 2001. *STATISTICA. System reference*. StatSoft Inc., Tulsa, Oklahoma, U.S.A. 1098 pp.

Statzner, B. 1981a. The relation between "hydraulic stress" and microdistribution of benthic macroinvertebrates in a lowland running water system, the Schierenseebrooks (North Germany). *Archiv für Hydrobiologie* 91(2): 192-218.

Statzner, B. 1981b. A method to estimate the population size of benthic macroinvertebrates in streams. *Oecologia* 51: 157-161.

Statzner, B. 1988. Growth and Reynolds number of lotic macroinvertebrates: a problem for adaptation of shape to drag. *Oikos* 51: 84-87.

Statzner, B. and Holm, T.F. 1982. Morphological adaptations of benthic invertebrates to stream flow - an old question studied by means of a new technique (laser doppler anemometry). *Oecologia* 53: 290-292.

Statzner, B. and Higler, B. 1985. Questions and comments on the continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1038-1044.

Statzner, B. and Higler, B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* 16: 127-139.

Statzner, B., Gore, J.A. and Resh, V.H. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* 7(4): 307-360.

Statzner, B. and Müller, R. 1989. Standard hemispheres as indicators of flow characteristics in lotic benthos research. *Freshwater Biology* 21: 445-459.

Statzner, B., Kohmann, F. and Schmedtje, U. 1990. A method of ecological appraisal for determining instream flow requirements in diverted streams. *Wasserwirtschaft* 80(5): 248-254.

Statzner, B., Kohmann, F. and Hildrew, A.G. 1991. Calibration of FST-hemispheres against bottom shear stress in a laboratory flume. *Freshwater Biology* 26: 227-231.

Statzner, B. and Borchardt, D. 1994. Longitudinal patterns and processes along streams: modelling ecological responses to physical gradients. Pp. 113-140. In: Giller, P.S., Hildrew, A.G. and Raffaelli, D.G. (eds). *Aquatic ecology. Scale, pattern and process.* The 34th Symposium of the British Ecological Society with the American Society of Limnology and Oceanography. University College, Cork, 1992. Blackwell Science Publications, Oxford, U.K. 649 pp.

Statzner, B., Hoppenhaus, K., Arens, M-F. and Richoux, P. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biology* 38: 109-135.

Stehr, W.C. and Branson, J.W. 1938. An ecological study of an intermittent stream. *Ecology* 19: 294-310.

Stewardson, M. and Gippel, C. 1997. In-stream environmental flow design: a review. *Technical Report for Hydro-Electric Corporation, Tasmania*. Cooperative Research Centre for Catchment Hydrology, Department of Civil and Environmental Engineering, University of Melbourne. Victoria, Australia. 99 pp.

Stewardson, M.J. and Gippel, C.J. 2003. Incorporating flow variability into environmental flow regimes using the Flow Events Method. *River Research and Applications* 19: 459-472.

Stewart-Oaten, A., Murdoch, W.W. and Parker, K.R. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67(4): 929-940.

Stromberg, J.C. and Patten, D.T. 1996. Instream flow and cottonwood growth in the eastern Sierra Nevada of California, USA. *Regulated Rivers: Research & Management* 12: 1-12.

Suren, A.M., Biggs, B.J.F., Duncan, M.J. and Bergey, L. 2003. Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment. 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research* 37: 71-83.

Swales, S., Bishop, K.A. and Harris, J.H. 1994. Assessment of environmental flows for native fish in the Murray-Darling Basin - a comparison of methods. Pp. 184-192. In: *Proceedings of Environmental Flows Seminar, Australian Water and Wastewater Association Inc*. Artarmon, N.S.W., Australia.

Swales, S. and Harris, J.H. 1995. The expert panel assessment method (EPAM): a new tool for determining environmental flows in regulated rivers. Pp. 125-134. In: Harper, D.M. and Ferguson, A.J.D. (eds). *The ecological basis for river management*. John Wiley and Sons, New York, U.S.A. 614 pp.

Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.

Taylor, R.C. 1983. Drought-induced changes in crayfish populations along a stream continuum. *American Midland Naturalist* 110: 286-298.

Tennant, D.L. 1976. Instream flow regimens for fish, wildlife, recreation and related environmental resources. *Fisheries* 1(4): 6-10.

Tharme, R.E. 1996. Review of international methodologies for the quantification of the instream flow requirements of rivers. *Water law review: final report for policy development*. For the Department of Water Affairs and Forestry, Pretoria. Freshwater Research Unit, University of Cape Town, South Africa. 116 pp.

Tharme, R.E. 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications* 19: 397-441.

Tharme, R.E. and C.A. Brown. 1994. Preliminary assessment of the ecological flow requirements of the Du Toit's River, Franschhoek. Final report to Cape Nature Conservation. Freshwater Research Unit, University of Cape Town, South Africa. 42 pp.

Tharme, R.E. and King, J.M. 1998. Development of the Building Block Methodology for instream flow assessments, and supporting research on the effects of different magnitude flows on riverine ecosystems. *Water Research Commission Report No.* 576/1/98. Water Research Commission, Pretoria, South Africa. 452 pp.

The Nature Conservancy (TNC). 2005. *User's manual for the indicators of Hydrologic Alteration (IHA) Software.* The Nature Conservancy, Charlottesville, Virginia, U.S.A.

The World Conservation Union (IUCN). 2000. *Vision for water and nature. A world strategy for conservation and sustainable management of water resources in the 21st century*. IUCN Gland, Switzerland and Cambridge, U.K.

Thomas, J.A. and Bovee, K.D. 1993. Application and testing of a procedure to evaluate transferability of habitat suitability criteria. *Regulated Rivers: Research & Management* 8: 285-294.

Thoms, M.C., Sheldon, F., Roberts, J., Harris, J. and Hillman, T.J. 1996. Scientific panel assessment of environmental flows for the Barwon-Darling River. Report to the Technical Services Division of the New South Wales Department of Land and Water Conservation. New South Wales, Australia. 161 pp.

Thoms, M.C. and Sheldon, F. 2000. Water resource development and hydrological change in a large dryland river: the Barwon-Darling River, Australia. *Journal of Hydrology* 228: 10-21.

Thoms, M.C. and Parsons, M. 2003. Identifying spatial and temporal patterns in the hydrological character of the Condamine-Balonne River, Australia, using multivariate statistics. *River Research and Applications* 19: 443-457.

Thorpe, J.H. and Delong, M.D. 1994. The riverine productivity model, an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* 70: 305-308.

Tickner, D., Armitage, P.D., Bickerton, M.A. and Hall, K.A. 2000. Assessing stream quality using information on mesohabitat distribution and character. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10: 179-196.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8: 36-50.

Townsend, C.R. and Hildrew, A.G. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology* 45: 759-772.

Townsend, CR, Hildrew, AG and Schofield, K. 1987. Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* 56: 597-613.

Townsend, C.R. and Hildrew, A.G. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* 31: 265-275.

Townsend, C.R., Scarsbrook, M.R. and Dolédec, S. 1997a. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society* 16(3): 531-544.

Townsend, C.R., Dolédec, S. and Scarsbrook, M.R. 1997b. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology* 37: 367-387.

Trihey, E.W. and Stalnaker, C.B. 1985. Evolution and application of instream flow methodologies to small hydropower developments: an overview of the issues. In: Olson, F.W., White, R.G. and Hamre, R.H. (eds). *Proceedings of the symposium on small hydropower and fisheries*. Aurora, Colorado, U.S.A.

Ubertini, L., Manciola, P. and Casadei, S. 1996. Evaluation of the minimum instream flow of the Tiber River Basin. *Environmental Monitoring and Assessment* 41: 125-136.

Ulfstrand, S. 1967. Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams. *Oikos* 18: 293-310.

Underwood, A.J. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Australian Journal of Ecology* 18: 99-116.

Underwood, A.J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4(1): 3-15.

United Nations World Water Assessment Programme. 2006. *Water: a shared responsibility. The United Nations World Water Development Report 2.* United Nations educational, Scientific and Cultural Organization (UNESCO), Paris, France, and Berghahn Books, New York, U.S.A. 584 pp.

Usinger, R.L. (ed.). 1956. *Aquatic insects of California with keys to North American genera and California species.* University of California Press, Berkeley, U.S.A. 508 pp.

Uys, M.C. and O'Keeffe, J.H. 1997a. Variability in the invertebrate fauna of an intermittent stream over three consecutive midsummer periods. *Southern African Journal of Aquatic Sciences* 23(2): 55-79.

Uys, M.C. and O'Keeffe, J.H. 1997b. Simple words and fuzzy zones: early directions for temporary river research in South Africa. *Environmental Management* 21(4): 517-531.

Vadas, R.L. Jr. and Orth, D.J. 1998. Use of physical variables to discriminate visually determined mesohabitat types in North American streams. *Rivers* 6(3): 143-159.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Viganò, L., Benedini, M., Badino, G., Barbiero, G., Buffagni, A., Pagnotta, R. and Spaggiari, R. 1997. Quantity and quality aspects in the protection of the aquatic environment. Country paper of Italy. Final draft. EurAqua 1997. Italy. 20 pp.

Voelz, N.J. and Ward, J.V. 1989. Biotic and abiotic gradients in a regulated high elevation Rocky Mountain river. *Regulated Rivers: Research & Management* 3: 143-152.

Vörösmarty, C.J., Sharma, K.P., Fekete, B.M., Copeland, A.H., Holden, J., Marble, J. and Lough, J.A. 1997. The storing and aging of continental runoff in large reservoir systems of the world. *Ambio* 26: 210-219.

Vörösmarty, C.J. and Sahagian, D. 2000. Anthropogenic disturbance of the terrestrial water cycle. *BioScience* 50(9): 753-765.

Vörösmarty, C.J., Green, P., Salisbury, J. and Lammers, R.B. 2000. Global water resources: vulnerability from climate change and population growth. *Science* 289: 284-288.

Waddle, T. 1998a. Development of 2-dimensional habitat models. Pp. 19-22. In: Blažková, Š., Stalnaker, C. and Novický, O. (eds). *Hydroecological modelling. Research, practice, legislation and decision-making*. Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Waddle, T. 1998b. Integrating microhabitat and macrohabitat. Pp. 12-14. In: Blažková, Š., Stalnaker, C. and Novický, O. (eds). *Hydroecological modelling. Research, practice, legislation and decision-making*. Report by US Geological Survey, Biological Research Division and Water Research Institute, Fort Collins, and Water Research Institute, Praha, Czech Republic. VUV, Praha, Czech Republic. 70 pp.

Wadeson, R.A. 1994. A geomorphological approach to the identification and classification of instream flow environments. *Southern African Journal of Aquatic Sciences* 20: 38-61.

Wadeson, R.A. 1996. The development of the hydraulic biotope concept within a catchment based hierarchical geomorphological model. Unpublished Ph.D. Thesis (submitted November 1995). Rhodes University. Grahamstown, South Africa. 320 pp.

Wadeson, R.A. and Rowntree, K.M. 1994. A hierarchical geomorphological model for the classification of South African river systems. Pp. 49-67. In: Uys, M.C. (ed.). Classification of rivers and environmental health indicators. Proceedings of a joint South African-Australian workshop. *Water Research Commission Report No.* TT 63/94. Water Research Commission, Pretoria, South Africa.

Wadeson, R.A. and Rowntree, K.M. 1998. Application of the hydraulic biotope concept to the classification of instream habitats. *Aquatic Ecosystem Health and Management* 1: 143-157.

Walker, K.F., Sheldon, F. and Puckridge, J.T. 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research & Management* 11: 85-104.

Wallace, J.B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. *Environmental Management* 14: 605-620.

Wang, L., Simonson, T.D. and Lyons, J. 1996. Accuracy and precision of selected stream habitat estimates. *North American Journal of Fisheries Management* 16: 340-347.

Ward, J.V. 1976. Effects of flow patterns below large dams on stream benthos: a review. Pp. 235-253. In: Orsborn, J.F. and Allman, C.H. (eds). *Instream flow needs symposium, Vol. II*. American Fisheries Society, Bethesda, Maryland, U.S.A.

Ward, J.A. 1982. Ecological aspects of stream regulation: responses in downstream lotic reaches. *Water pollution and Management Reviews (New Delhi)* 2: 1-26.

Ward, J.V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8(1): 2-8.

Ward, J.V. and Short, R.A. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, U.S.A. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 20: 1382-1387.

Ward, J.W. and Stanford, J.A. (eds). 1979. *The ecology of regulated streams*. Plenum Press, New York, U.S.A. 398 pp.

Ward, J.V. and Stanford, J.A. 1983a. The serial discontinuity concept of lotic ecosystems. Pp 29-42. In: Fontaine, T.D. III and Bartell, S.M. (eds). *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers, Ann Arbor, Michigan, U.S.A. 494 pp.

Ward, J.V. and Stanford, J.A. 1983b. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pp. 347-356. In: Fontaine, T.D. III and Bartell, S.M. (eds). *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers, Ann Arbor, Michigan, U.S.A. 494 pp.

Ward, J.V. and Stanford, J.A. 1987. The ecology of regulated streams: past accomplishments and directions for future research. Pp 391-409. In: Craig, J.F. and Kemper, J.B. (eds). *Regulated streams: advances in ecology*. Plenum Press, New York, U.S.A.

Ward, J.V. and Stanford, J.A. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research & Management* 11: 105-119.

Washington, H.G. 1984. Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. *Water Research* 18(6): 653-694.

Waters, B.F. 1976. A methodology for evaluating the effects of different stream flows on salmonid habitat. In: Orsborn, J.F. and Allman, C.H. (eds). *Symposium on instream flow needs*. American Fisheries Society, Bethseda, Maryland, U.S.A.

Webster, J.R., Gurtz, M.E., Hains, J.J., Meyer, J.L., Swank, W.T., Waide, J.B. and Wallace, J.B. 1983. Stability of stream ecosystems. Pp. 355-395. In: Barnes, J.R. and Minshall, G.W. (eds). *Stream ecology. Application and testing of general ecological theory*. Plenum Press, New York, U.S.A. 399 pp.

Weeks, D.C., O'Keeffe, J.H., Fourie, A. and Davies, B.R. 1996. A pre-impoundment study of the Sabie-Sand river system, Mpumalanga with special reference to predicted impacts on the Kruger National Park. Volume One. The ecological status of the Sabie-Sand River system. *Water Research Commission Report No.* 294/1/96. Pretoria, South Africa. 259 pp.

Weisberg, S.B., Janicki, A.J., Gerritsen, J. and Wilson, H.T. 1990. Enhancement of benthic macroinvertebrates by minimum flow from a hydroelectric dam. *Regulated Rivers: Research & Management* 5:265-277.

Welcomme, R.L. (Compiler). 2001. *Inland fisheries. Ecology and management*. United Nations Food and Agriculture Organization. Fishing News Books, Blackwell Science, Oxford, U.K. 358 pp.

Wesche, T.A. and Rechard, P.A. 1980. A summary of instream flow methods for fisheries and related needs. *Eisenhower Consortium Bulletin No*. 9. Produced for the U.S.D.A. Forest Service. Water Resources Research Institute, University of Wyoming, U.S.A.

Wetmore, S.H., Mackay, R.J. and Newbury, R.W. 1990. Characterization of the hydraulic habitat of *Brachycentrus occidentalis*, a filter feeding caddisfly. *Journal of the North American Benthological Society* 9: 157-169.

White, P.S. and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. Pp. 3-13. In: Pickett, S.T.A. and White, P.S. (eds). *The ecology of natural disturbance and patch dynamics*. Academic Press, Inc., Orlando, U.S.A. 472 pp.

Whittington, J. 2000. Development of relationships between flow regime and river health. Outcomes of a joint Cooperative Research Centre for Freshwater Ecology and Queensland Department of Natural Resources workshop. *Technical Report No.* 6/2000. Cooperative Research Centre for Freshwater Ecology, University of Canberra, ACT, Australia. 25 pp.

Wiederholm, T. (ed.) 1983. Chironomidae of the Holarctic region. Keys and diagnosis. Part 1. Larvae. *Entomologica Scandinavica Supplement No*. 19.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Williams, D.D. 1980. Some relationships between stream benthos and substrate heterogeneity. *Limnology and Oceanography* 25: 166-172.

Williams, D.D. 1984. The hyporheic zone as a habitat for aquatic insects and associated arthropods. Pp. 430-455. In: Resh, V.H. and Rosenberg, D.M. (eds). *The ecology of aquatic insects*. Praeger Scientific, New York, U.S.A.

Williams, D.D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. *Journal of the North American Benthological Society* 15: 634-650.

Williams, D.D.and Hynes, H.B.N. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27: 265-272.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue der gesamten Hydrobiologie* 62: 53-61.

Williams, R.D. and Winget, R.N. 1979. Macroinvertebrate response to flow manipulation in the Strawberry River, Utah (U.S.A.). Pp. 365-376. In: Ward, J.V. and Stanford, J.A. (eds). *The ecology of regulated streams*. Plenum Press, New York and London, U.S.A. and U.K.

Williamson, S.C., Bartholow, J.M. and Stalnaker, C.B. 1993. Conceptual model for quantifying pre-smolt production from flow-dependent physical habitat and water temperature. *Regulated Rivers: Research & Management* 8: 15-28.

Windt, N. 1993. Methods of water quality analysis. Internal Technical Report. Council for Scientific and Industrial Research, EMATEK, Stellenbosch, South Africa.

Winterbottom, J.H., Orton, S.E. and Hildrew, A.G. 1997. Field experiments on the mobility of benthic invertebrates in a southern English stream. *Freshwater Biology* 38: 37-47.

Wishart, M.J. 2000. Catchments as conservation units for riverine biodiversity. *African Journal of Aquatic Science* 25 (1): 169–174.

Wishart, M.J. and Day, J.A. 2002. Endemism in the freshwater fauna of the south-western Cape, South Africa. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 28: 1-5.

With, K.A. and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76: 2446-2459.

With, K.A., Gardner, R.H. and Turner, M.G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78: 151-169.

Wohl, D.L., Wallace, J.B. and Meyer, J.L. 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). *Freshwater Biology* 34: 447-464.

Wood, P.J. and Petts, G.E. 1994. Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research & Management* 9: 303-316.

Wood, P.J. and Petts, G.E. 1999. The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes* 13: 387-399.

Wood, P.J., Armitage, P.D., Cannan, C.E. and Petts, G.E. 1999. Instream mesohabitat biodiversity in three groundwater streams under base-flow conditions. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9: 265-278.

Wood, P.J., Agnew, M.D. and Petts, G.E. 2000. Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes* 14: 3133-3147.

Wootton, J.T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. *The American Naturalist* 152(6): 803-825.

World Commission on Dams (WCD). 2000. *Dams and development. A new framework for decision-making. The report of the World Commission on Dams.* Earthscan Publications Ltd., London, U.K. and Sterling, VA, U.S.A. 404 pp.

World Resources Institute (WRI). 1998. *World Resources*: *1998-99*. Oxford University Press, New York, U.S.A.

Wright, J.F., Hiley, P.D., Cooling, D.A., Cameron, A.C., Wigham, M.E. and Berrie, A.D. 1984. The invertebrate fauna of a small chalk stream in Berkshire, England, and the effect of intermittent flow. *Archiv für Hydrobiologie* 99: 176-199.

Wright, J.F. and Berrie, A.D. 1987. Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research & Management* 1: 145-160.

Wright, J.F., Blackburn, J.H., Gunn, R.J.M., Furse, M.T., Armitage, P.D., Winder, J.M. and Symes, K.L. 1996. Macroinvertebrate frequency data for the RIVPACS III sites in Great Britain and their use in conservation evaluation. *Aquatic Conservation* 6: 141-167.

Wu, J. and Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology* 70: 439-466.

Young, W.J. 1992. Classification of the criteria used to identify near-bed flow regimes. *Freshwater Biology* 28: 383-391.

Yount, J.D. and Niemi, G.J. 1990. Recovery of lotic communities and ecosystems from disturbance - a narrative review of case studies. *Environmental Management* 14(5): 547-569.

Yu, S. and Peters, E.J. 1997. Use of Froude number to determine habitat selection by fish. *Rivers* 6(1): 10-18.

Zalewski, M. 2000. Ecohydrology - the scientific background to use ecosystem properties as management tools toward sustainability of water resources. *Ecological Engineering* 16(1): 1-8.

Zalewski, M. 2002. Ecohydrology - the use of ecological and hydrological processes for sustainable management of water resources. *Hydrological Sciences Journal* 47: 825-834.

Zar, J.H. 1984. *Biostatistical analysis. Second edition.* Prentice-Hall Inc., New Jersey, U.S.A. 718 pp.

Zwick, P. 1992. Stream habitat fragmentation. A threat to biodiversity. *Biodiversity and Conservation* 1: 80-97.

APPENDICES

Appendix 2.1 **Shortlist of 32 hydrological gauging weirs visited between January and February 1994.** The extent to which the weirs fulfilled selection criteria (Table 2.1) is summarised. Unless otherwise specified, the weirs are managed by DWAF. Weir types are designated: NW = weir recording natural/near-natural streamflow; NW+A = weir measuring an in-channel flow regime reflecting run-of-river abstraction; DW = weir at which a proportion of the flow is being diverted. General flow record and habitat suitability, and the extent of anthropogenic influence, are rated as L = Low; M = Moderate; H = High; or a range. "?" denotes uncertainty, with information lacking at the time of survey. CNC = Cape Nature Conservation; CPA = Cape Provincial Administration; SAFCOL = South African Forestry Company Limited.

WEIR NO.	RIVER	LOCATION	LATITUDE	LONGITUDE	WEIR TYPE	SUITABILITY OF HISTORICAL FLOW RECORD	FLOW RECORDS OF ABSTRACTION VOLUME	DEGREE OF ANTHROPOGENIC DISTURBANCE	SUITABILITY OF RIVER REACH & INSTREAM PHYSICAL HABITAT	FLOW CONDITION
G1H003	**Franschhoek**	La Provence, near Robertsvlei	33º53'26"	19º04'44"	NW+A	L-M	-	H	L	Very low flow
G1H008	**Klein-Berg**	Nieuwkloof, near Tulbagh	33º18'41"	19º04'31"	NW+A (& downstream diversion canal)	L-M	Yes?	H	M	Very low flow
G1H010	**Knolvleispruit**	Knolvlei Bos. Res.	33º23'24"	19º09'35"	NW	M?	-	M-H	L	Zero flow; intermittent river
G1H012	**Watervals**	Watervalsberge, Watervals-Onder	33º21'08"	19º06'04"	DW (small offtake canal)	H	N	M	L	Zero flow
G1H014	**Zachariashoek**	Zachariashoek, near Wemmershoek Dam	33º49'39"	19º02'08"	NW	M?	-	L	M	Flowing well
G1H016	**Kasteelskloof**	Zachariashoek, near Wemmershoek Dam	33º49'19"	19º03'35"	NW	M?	-	L	M	Flowing well
G1H018	**Bakkerskloof**	Zachariashoek, near Wemmershoek Dam	33º49'21"	19º02'50"	NW	M?	-	L	M	Flowing well

Appendix 2.1 Continued.

WEIR NO.	RIVER	LOCATION	LATITUDE	LONGITUDE	WEIR TYPE	SUITABILITY OF HISTORICAL FLOW RECORD	FLOW RECORDS OF ABSTRACTION VOLUME	DEGREE OF ANTHROPOGENIC DISTURBANCE	SUITABILITY OF RIVER REACH & INSTREAM PHYSICAL HABITAT	FLOW CONDITION
G1H019	**Banghoek**	Jonkershoek, The Sanctuary	33º54'44"	18º56'36"	NW+A	H	-	M	M	Flowing well
G1H028	**Twenty-four**	Drie-Das-Bosch, near Voëlvlei Dam	33º08'02"	19º03'39"	DW	L-M	Yes?	M	M-H	No flow, only weir leakage
G1H029	**Leeu**	De Hoek Estates farm, near Voëlvlei Dam	33º09'24"	19º03'08"	DW (G1H059 is canal)	H	Yes?	M-H	M	No flow, only weir leakage
G1H042	**Banghoek**	Bosmanshoek	33º57'10"	18º58'45"	DW (& downstream weir)	H	N	M-H	H	Flowing well
G2H007	**Lang**	Jonkershoek Valley, near Stellenbosch	33º59'13"	18º58'13"	NW	H	-	L	H	Flowing well
G2H008	**Eerste**	Jonkershoek Valley, upstream of Kleinplaas Dam, near Stellenbosch	33º59'11"	18º57'23"	DW	L-M	Y	M-H	M-H	Dry bed, slight weir leakage
G4H014	**Bot**	Roode Heuvel, at N2 road bridge	34º12'25"	19º14'06"	NW+A	M-H?	-	H	L	Slow flow
HIH006	**Breë**	Witbrug, Mitchells Pass road, near Ceres	33º25'18"	19º16'06"	DW	M?	Y	M-H	H	Mostly dry bed, slight weir leakage
H1H017 & H1H033	**Elands**	Hawequas Bos Res., Du Toit's Kloof Valley	33º44'05"	19º06'54"	NW	M-H	-	L	H	Flowing well
H1H018	**Molenaars**	Hawequas Bos Res., Du Toit's Kloof Valley	33º43'24"	19º10'13"	NW	M-H	-	L	H	Flowing well
H2H003	**Hex**	De Wet, near Worcester	33º36'00"	19º30'33"	DW	M?	N	M-H	M	Mostly dry bed, very low flow

Appendix 2.1 Continued.

WEIR NO.	RIVER	LOCATION	LATITUDE	LONGITUDE	WEIR TYPE	SUITABILITY OF HISTORICAL FLOW RECORD	FLOW RECORDS OF ABSTRACTION VOLUME	DEGREE OF ANTHROPOGENIC DISTURBANCE	SUITABILITY OF RIVER REACH & INSTREAM PHYSICAL HABITAT	FLOW CONDITION
H2H006	**Hex**	Glen Heatlie, near Worcester	33º34'39"	19º30'12"	NW	M?	-	H	M	Flowing well
H6H006	**Elands**	Twist Niet, Radyn, near Villiersdorp	33º57'53"	19º17'32"	NW+A (side DW not in use)	L	N	H	L	Low flow
H6H007	**Du Toits**	Purgatory Outspan, Franschhoek Pass	33º56'19"	19º10'17"	NW	L-M	-	L	H	Flowing well
H6H008	**Riviersonderend**	Swarte Water, Nuweberg Bos Res., upstream of Theewaterskloof Dam	34º03'44"	19º04'23"	NW	M-H	-	L	H	Flowing well
H6H010	**Waterkloof**	Waggensbooms Kloof, Wolwekloof Farm, near Villiersdorp	33º59'00"	19º19'48"	NW+A	H	-	L	L-M	Flowing well
Groenberg weirs (CPA/SAFCOL Forestry)	**Five adjacent streams**	Groenlandberge, SAFCOL plantation, near Houhoek	*c.* 34º10'41"	19º07'45"	NW	?	-	M	L-M	Zero to very low flow; rivers seasonal?
Heuningkloof weir (CNC/Forestry)	**Heuningkloof**	Heuningkloof, Jonkershoek Valley	33º57'58"	18º57'32"	DW	No record	N	L	L-M	Low flow
Lambrechtsbos weir (CNC/Forestry)	**Lambrechtskloof**	Lambrechtskloof, Jonkershoek Valley	33º57'54"	18º56'37"	NW	H?	-	L	L-M	Low flow
Sosyskloof weir (CNC/Forestry)	**Sosyskloof**	Sosyskloof, Jonkershoek Valley	33º59'24"	18º57'08"	DW	No record	N	L	M-H	Very low flow, from weir leakage
Swartboskloof weir (CNC/Forestry)	**Swartboskloof**	Swartboskloof, Jonkershoek Valley	33º59'30"	18º57'21"	NW	L?	-	L	M-H	Flowing well

Appendix 2.2 **Means ± SDs of benthic macroinvertebrate abundances per 0.1 m^2 of riffle for the eight sites (*n* = 6; shaded columns) and locations within each of them (*n* = 3), March 1994. EL - Elands; MO - Molenaars.** 1 - upstream location; 2 - downstream location. M - mean abundance per site. L - larva; P - pupa; A - adult; L+P - combination, where larvae represent the majority in all instances.

FAMILY/TAXON	EL 1	SD	EL 2	SD	EL M	SD	MO 1	SD	MO 2	SD	MO M	SD
ACARINA	15.0	± 7.9	36.0	± 21.0	25.5	± 18.3	38.3	± 14.3	21.3	± 14.0	29.8	± 15.7
AMPHIPODA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
COLEOPTERA:												
Dryopidae (A)	0.7	±1.2	0.7	± 1.2	0.7	± 1.0	2.0	± 1.7	1.3	± 1.5	1.7	± 1.5
Elmidae (A)	4.3	± 3.2	3.7	± 2.5	4.0	± 2.6	8.7	± 6.1	16.7	± 25.4	12.7	± 17.1
Elmidae (L)	50.7	± 18.7	66.0	± 23.4	58.3	± 20.7	15.7	± 3.8	21.3	± 24.8	18.5	± 16.2
Gyrinidae (L)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.7	± 1.2	0.3	± 0.8
Helodidae (L)	3.0	± 2.6	1.0	± 1.7	2.0	± 2.3	2.7	± 2.1	0.3	± 0.6	1.5	± 1.9
Hydraenidae (A)	2.7	± 2.1	6.0	± 1.0	4.3	± 2.3	38.0	± 27.9	54.0	± 77.4	46.0	± 52.8
Limnichidae (L)	0.7	± 1.2	0.7	± 1.2	0.7	± 1.0	95.3	± 89.6	25.7	± 32.3	60.5	± 71.3
COLLEMBOLA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
DIPTERA:												
Blepharoceridae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ceratopogonidae	0.7	± 1.2	0.0	± 0.0	0.3	± 0.8	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4
Chironomidae (L+P)	447.0	± 236.8	443.0	± 177.2	445.0	± 187.1	750.0	± 258.7	655.0	± 283.5	702.5	± 248.3
Dixidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Empididae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4
Athericidae	4.7	± 3.5	8.7	± 7.4	6.7	± 5.6	11.7	± 6.5	10.3	± 15.3	11.0	± 10.5
Simuliidae (L+P)	10.0	± 10.5	22.3	± 18.5	16.2	± 15.1	685.3	± 405.0	2012.3	± 2052.9	1348.8	± 1509.8
Stratiomyidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Tipulidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
EPHEMEROPTERA:												
Baetidae	403.0	± 270.5	505.3	± 185.7	454.2	± 214.9	699.0	± 127.0	439.0	± 219.2	569.0	± 214.4
Caenidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	5.7	± 9.8	1.3	± 2.3	3.5	± 6.8
Teloganodidae	57.0	± 31.6	58.7	± 49.2	57.8	± 37.0	11.0	± 5.6	15.7	± 16.8	13.3	± 11.5
Heptageniidae	10.7	± 8.5	14.7	± 14.5	12.7	± 10.9	8.7	± 6.4	4.7	± 1.2	6.7	± 4.7
Leptophlebiidae	18.0	± 18.0	48.7	± 60.5	33.3	± 43.3	477.3	± 214.6	273.3	± 382.4	375.3	± 299.0
Tricorythidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
HEMIPTERA:												
Corixidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.3	± 2.3	0.7	± 1.2	1.0	± 1.7
Gerridae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Veliidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
LEPIDOPTERA:												
Pyraustidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	3.0	± 1.7	1.7	± 2.1	2.3	± 1.9
MEGALOPTERA:												
Corydalidae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.7	± 0.6	2.7	± 3.8	1.7	± 2.7
NEMATODA	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	3.0	± 3.0	2.3	± 2.3	2.7	± 2.4
ODONATA:												
Coenagrionidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Aeshnidae	0.3	± 0.6	0.3	± 0.6	0.3	± 0.5	0.7	± 0.6	0.3	± 0.6	0.5	± 0.5
Libellulidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4
OLIGOCHAETA	38.3	± 23.4	25.0	± 30.3	31.7	± 25.3	4.0	± 1.7	6.0	± 7.2	5.0	± 4.8
PLATYHELMINTHES	1.3	± 2.3	1.7	± 2.1	1.5	± 2.0	3.7	± 2.3	5.7	± 6.7	4.7	± 4.6
PLECOPTERA:												
Notonemouridae	1.0	± 1.0	1.7	± 0.6	1.3	± 0.8	0.3	± 0.6	0.3	± 0.6	0.3	± 0.5
TRICHOPTERA:												
Barbarochthonidae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ecnomidae	0.0	± 0.0	1.3	± 2.3	0.7	± 1.6	0.3	± 0.6	2.7	± 4.6	1.5	± 3.2
Glossosomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Hydropsychidae (L+P)	67.7	± 48.3	60.3	± 40.6	64.0	± 40.1	164.3	± 46.7	119.0	± 69.7	141.7	± 58.6
Hydroptilidae (L+P)	1.3	± 2.3	0.3	± 0.6	0.8	± 1.6	0.0	± 0.0	1.3	± 2.3	0.7	± 1.6
Leptoceridae	0.0	± 0.0	0.7	± 1.2	0.3	± 0.8	4.7	± 4.0	4.7	± 6.4	4.7	± 4.8
Petrothrincidae (L+P)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Philopotamidae	15.3	± 9.0	41.3	± 27.3	28.3	± 23.1	29.3	± 21.5	31.3	± 16.7	30.3	± 17.2
Sericostomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0

Appendix 2.2 Continued. RI - Riviersonderend; ZA - Zachariashoek.

FAMILY/TAXON	RI 1	SD	RI 2	SD	RI M	SD	ZA 1	SD	ZA 2	SD	ZA M	SD
ACARINA	19.3	± 5.1	18.7	± 9.5	19.0	± 6.8	8.3	± 11.0	2.7	± 3.8	5.5	± 8.0
AMPHIPODA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.7	± 1.2	0.3	± 0.6	0.5	± 0.8
COLEOPTERA:												
Dryopidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Elmidae (A)	6.3	± 3.2	2.0	± 2.6	4.2	± 3.5	8.0	± 13.0	1.3	± 1.5	4.7	± 9.0
Elmidae (L)	45.0	± 16.5	81.0	± 27.0	63.0	± 28.1	26.3	± 37.8	8.7	± 4.6	17.5	± 26.0
Gyrinidae (L)	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	1.0	± 1.0	0.0	± 0.0	0.5	± 0.8
Helodidae (L)	15.0	± 14.1	4.0	± 2.6	9.5	± 10.9	1.7	± 2.1	3.7	± 5.5	2.7	± 3.9
Hydraenidae (A)	5.3	± 7.6	3.0	± 3.0	4.2	± 5.3	63.0	± 91.8	50.0	± 77.9	56.5	± 76.5
Limnichidae (L)	0.3	± 0.6	1.3	± 1.5	0.8	± 1.2	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
COLLEMBOLA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
DIPTERA:												
Blepharoceridae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ceratopogonidae	1.3	± 2.3	2.3	± 3.2	1.8	± 2.6	2.3	± 1.5	2.7	± 2.1	2.5	± 1.6
Chironomidae (L+P)	707.7	± 19.5	464.0	± 186.1	585.8	± 178.4	113.0	± 78.5	192.0	± 128.0	152.5	± 104.4
Dixidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
Empididae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.7	± 2.1	1.0	± 1.0	1.3	± 1.5
Athericidae	5.3	± 2.9	6.7	± 2.5	6.0	± 2.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Simuliidae (L+P)	46.0	± 26.1	17.0	± 13.0	31.5	± 24.3	2.7	± 2.1	13.3	± 19.7	8.0	± 13.8
Stratiomyidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Tipulidae	0.7	± 0.6	0.0	± 0.0	0.3	± 0.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
EPHEMEROPTERA:												
Baetidae	99.0	± 71.1	70.0	± 24.1	84.5	± 50.1	15.0	± 13.0	17.3	± 14.5	16.2	± 12.4
Caenidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.7	± 1.2	0.7	± 1.2	0.7	± 1.0
Teloganodidae	5.3	± 4.0	2.3	± 2.1	3.8	± 3.3	21.7	± 15.6	9.0	± 12.1	15.3	± 14.3
Heptageniidae	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
Leptophlebiidae	38.3	± 42.5	23.3	± 14.6	30.8	± 29.6	4.3	± 5.1	7.0	± 11.3	5.7	± 8.0
Tricorythidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.3	± 0.6	3.3	± 4.9	1.8	± 3.5
HEMIPTERA:												
Corixidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Gerridae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Veliidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
LEPIDOPTERA:												
Pyraustidae	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
MEGALOPTERA:												
Corydalidae	0.7	± 1.2	0.3	± 0.6	0.5	± 0.8	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
NEMATODA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.0	± 0.0	1.0	± 1.0	1.0	± 0.6
ODONATA:												
Coenagrionidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.7	± 0.6	0.0	± 0.0	0.3	± 0.5
Aeshnidae	0.0	± 0.0	0.7	± 0.6	0.3	± 0.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Libellulidae	0.3	± 0.6	0.7	± 1.2	0.5	± 0.8	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
OLIGOCHAETA	46.0	± 36.1	93.3	± 102.8	69.7	± 73.6	54.0	± 15.9	111.3	± 150.7	82.7	± 100.9
PLATYHELMINTHES	2.3	± 4.0	0.0	± 0.0	1.2	± 2.9	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
PLECOPTERA:												
Notonemouridae	7.3	± 6.5	1.7	± 1.2	4.5	± 5.2	41.3	± 49.2	28.7	± 42.8	35.0	± 41.9
TRICHOPTERA:												
Barbarochthonidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ecnomidae	0.7	± 1.2	1.7	± 2.1	1.2	± 1.6	4.3	± 3.1	1.0	± 1.0	2.7	± 2.7
Glossosomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Hydropsychidae (L+P)	2.0	± 1.0	2.7	± 1.5	2.3	± 1.2	7.3	± 8.7	10.3	± 11.4	8.8	± 9.2
Hydroptilidae (L+P)	0.7	± 1.2	1.7	± 1.5	1.2	± 1.3	0.7	± 1.2	0.7	± 1.2	0.7	± 1.0
Leptoceridae	19.7	± 14.6	16.7	± 5.7	18.2	± 10.1	0.7	± 1.2	0.0	± 0.0	0.3	± 0.8
Petrothrincidae (L+P)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Philopotamidae	1.0	± 1.0	0.3	± 0.6	0.7	± 0.8	1.7	± 1.5	1.7	± 2.9	1.7	± 2.1
Sericostomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4

Appendix 2.2 Continued. DU - Du Toits; LA - Langrivier.

FAMILY/TAXON	DU 1	SD	DU 2	SD	DU M	SD	LA 1	SD	LA 2	SD	LA M	SD
ACARINA	19.0	± 11.1	7.0	± 4.0	13.0	± 10.0	2.3	± 2.5	1.7	± 1.5	2.0	± 1.9
AMPHIPODA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
COLEOPTERA:												
Dryopidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Elmidae (A)	2.3	± 1.5	1.0	± 1.0	1.7	± 1.4	0.3	± 0.6	1.7	± 1.2	1.0	± 1.1
Elmidae (L)	29.3	± 15.5	25.0	± 17.7	27.2	± 15.1	4.3	± 3.1	4.7	± 1.5	4.5	± 2.2
Gyrinidae (L)	0.0	± 0.0	0.7	± 0.6	0.3	± 0.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Helodidae (L)	2.3	± 2.3	1.0	± 1.0	1.7	± 1.8	4.3	± 4.0	14.7	± 2.1	9.5	± 6.3
Hydraenidae (A)	19.7	± 30.6	5.3	± 1.2	12.5	± 20.9	0.0	± 0.0	2.3	± 1.2	1.2	± 1.5
Limnichidae (L)	1.3	± 0.6	2.0	± 3.5	1.7	± 2.3	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
COLLEMBOLA	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	0.7	± 0.6	0.7	± 1.2	0.7	± 0.8
DIPTERA:												
Blepharoceridae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.7	± 0.6	0.3	± 0.5
Ceratopogonidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.3	± 0.6	0.7	± 1.2	1.0	± 0.9
Chironomidae (L+P)	645.0	± 151.9	637.7	± 312.8	641.3	± 219.9	81.0	± 41.6	101.3	± 42.8	91.2	± 39.3
Dixidae	0.0	± 0.0	0.7	± 1.2	0.3	± 0.8	0.3	± 0.6	0.7	± 0.6	0.5	± 0.5
Empididae	1.7	± 2.9	0.7	± 0.6	1.2	± 1.9	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
Athericidae	8.0	± 7.9	10.7	± 10.8	9.3	± 8.6	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Simuliidae (L+P)	224.3	± 233.0	134.3	± 175.6	179.3	± 191.0	25.0	± 11.4	62.3	± 41.0	43.7	± 33.8
Stratiomyidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.7	± 1.2	0.3	± 0.6	0.5	± 0.8
Tipulidae	0.7	± 1.2	0.3	± 0.6	0.5	± 0.8	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
EPHEMEROPTERA:												
Baetidae	31.0	± 12.5	34.7	± 11.0	32.8	± 10.7	31.0	± 21.0	46.7	± 14.4	38.8	± 18.3
Caenidae	20.3	± 35.2	2.0	± 2.0	11.2	± 24.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Teloganodidae	15.7	± 24.5	9.7	± 9.3	12.7	± 16.9	3.0	± 1.7	6.7	± 6.4	4.8	± 4.6
Heptageniidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Leptophlebiidae	3.7	± 3.5	0.3	± 0.6	2.0	± 2.9	9.0	± 6.0	25.0	± 14.5	17.0	± 13.3
Tricorythidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
HEMIPTERA:												
Corixidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Gerridae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Veliidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.3	± 0.6	0.7	± 0.8
LEPIDOPTERA:												
Pyraustidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
MEGALOPTERA:												
Corydalidae	0.3	± 0.6	0.7	± 0.6	0.5	± 0.5	1.0	± 1.0	1.3	± 1.5	1.2	± 1.2
NEMATODA	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
ODONATA:												
Coenagrionidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Aeshnidae	0.3	± 0.6	0.3	± 0.6	0.3	± 0.5	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
Libellulidae	0.0	± 0.0	1.0	± 0.0	0.5	± 0.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
OLIGOCHAETA	14.3	± 11.8	23.7	± 29.7	19.0	± 20.9	6.7	± 5.0	37.0	± 21.0	21.8	± 21.5
PLATYHELMINTHES	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
PLECOPTERA:												
Notonemouridae	6.7	± 6.0	10.7	± 7.2	8.7	± 6.3	10.0	± 9.5	10.7	± 4.0	10.3	± 6.6
TRICHOPTERA:												
Barbarochthonidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ecnomidae	1.7	± 2.9	0.3	± 0.6	1.0	± 2.0	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4
Glossosomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	2.3	± 2.1	2.7	± 3.1	2.5	± 2.3
Hydropsychidae (L+P)	1.3	± 1.2	1.7	± 1.5	1.5	± 1.2	2.7	± 2.5	5.3	± 2.5	4.0	± 2.7
Hydroptilidae (L+P)	7.7	± 9.3	13.3	± 15.4	10.5	± 11.8	2.3	± 3.2	2.3	± 2.5	2.3	± 2.6
Leptoceridae	6.0	± 5.0	4.3	± 4.5	5.2	± 4.4	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4
Petrothrincidae (L+P)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Philopotamidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	2.7	± 2.1	2.0	± 1.0	2.3	± 1.5
Sericostomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4

Appendix 2.2 Continued. BA - Bakkerskloof; HE - Hex.

FAMILY/TAXON	BA 1	SD	BA 2	SD	BA M	SD	HE 1	SD	HE 2	SD	HE M	SD
ACARINA	2.7	± 2.5	0.7	± 1.2	1.7	± 2.1	4.0	± 4.0	1.3	± 2.3	2.7	± 3.3
AMPHIPODA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
COLEOPTERA:												
Dryopidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Elmidae (A)	6.0	± 5.6	1.7	± 2.9	3.8	± 4.6	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Elmidae (L)	127.3	± 103.7	45.0	± 45.9	86.2	± 84.7	2.7	± 2.3	0.0	± 0.0	1.3	± 2.1
Gyrinidae (L)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Helodidae (L)	59.0	± 48.1	17.3	± 18.8	38.2	± 39.9	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Hydraenidae (A)	9.7	± 5.5	6.0	± 4.6	7.8	± 5.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Limnichidae (L)	0.7	± 0.6	0.3	± 0.6	0.5	± 0.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
COLLEMBOLA	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
DIPTERA:												
Blepharoceridae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ceratopogonidae	5.3	± .6	0.7	± 0.6	3.0	± 3.9	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Chironomidae (L+P)	75.0	± 33.2	52.3	± 25.9	63.7	± 29.4	146.7	± 56.8	405.3	± 84.9	276.0	± 155.7
Dixidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Empididae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Athericidae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Simuliidae (L+P)	11.7	± 15.3	3.0	± 4.4	7.3	± 11.1	5.3	± 9.2	32.0	± 28.8	18.7	± 24.1
Stratiomyidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Tipulidae	0.7	± 0.6	0.0	± 0.0	0.3	± 0.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
EPHEMEROPTERA:												
Baetidae	27.3	± 34.6	7.3	± 1.5	17.3	± 24.5	293.3	± 74.3	268.0	± 114.8	280.7	± 87.6
Caenidae	3.0	± 5.2	0.0	± 0.0	1.5	± 3.7	0.0	± 0.0	2.7	± 4.6	1.3	± 3.3
Teloganodidae	32.7	± 10.1	132.0	± 84.8	82.3	± 76.7	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Heptageniidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	121.3	± 89.9	68.0	± 65.5	94.7	± 76.2
Leptophlebiidae	36.0	± 12.5	36.0	± 21.5	36.0	± 15.7	8.0	± 6.9	238.7	± 180.1	123.3	± 170.1
Tricorythidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	190.7	± 80.1	305.3	± 246.0	248.0	± 175.3
HEMIPTERA:												
Corixidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.3	± 2.3	0.0	± 0.0	0.7	± 1.6
Gerridae (A)	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Veliidae (A)	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
LEPIDOPTERA:												
Pyraustidae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
MEGALOPTERA:												
Corydalidae	0.0	± 0.0	0.3	± 0.6	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
NEMATODA	0.0	± 0.0	1.0	± 1.0	0.5	± 0.8	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
ODONATA:												
Coenagrionidae	1.0	± 1.0	0.7	± 1.2	0.8	± 1.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Aeshnidae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.0	± 0.0	1.3	± 2.3	0.7	± 1.6
Libellulidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
OLIGOCHAETA	25.7	± 10.0	4.0	± 6.1	14.8	± 14.0	0.0	± 0.0	37.3	± 47.4	18.7	± 36.3
PLATYHELMINTHES	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	1.3	± 2.3	0.0	± 0.0	0.7	± 1.6
PLECOPTERA:												
Notonemouridae	34.7	± 13.4	48.0	± 37.6	41.3	± 26.3	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
TRICHOPTERA:												
Barbarochthonidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Ecnomidae	4.0	± 2.6	5.7	± 3.2	4.8	± 2.8	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Glossosomatidae	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Hydropsychidae (L+P)	3.0	± 3.0	0.0	± 0.0	1.5	± 2.5	80.0	± 18.3	121.3	± 72.6	100.7	± 52.5
Hydroptilidae (L+P)	0.0	± 0.0	1.7	± 1.5	0.8	± 1.3	0.0	± 0.0	8.0	± 4.0	4.0	± 5.1
Leptoceridae	3.3	± 2.5	3.0	± 3.0	3.2	± 2.5	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Petrothrincidae (L+P)	1.7	± 1.5	1.0	± 1.0	1.3	± 1.2	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Philopotamidae	0.3	± 0.6	0.0	± 0.0	0.2	± 0.4	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0
Sericostomatidae	0.7	± 1.2	1.0	± 1.7	0.8	± 1.3	0.0	± 0.0	0.0	± 0.0	0.0	± 0.0

Appendix 2.3 **Results of a SIMPER analysis comparing the average taxon abundances (0.1 m^{-2}) among all eight sites.** $\overline{\delta}_i$ = the contribution of the *i*th taxon to overall average dissimilarity ($\overline{\delta}$) between sites, expressed as a cumulative percentage ($\Sigma \overline{\delta}_i$ %). Taxa are listed in order of decreasing contribution to dissimilarity, with an arbitrary cutoff below 50% dissimilarity.

$\overline{\delta}$ **BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA**	**AVERAGE ABUNDANCE (0.1 m^{-2})**		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ **%**	$\Sigma \overline{\delta}_i$ **%**
EL and MO = 29.45 %	EL	MO				
Simuliidae (L+P)	16.17	1348.83	4.54	2.08	15.42	15.42
Leptophlebiidae	33.33	375.33	2.19	1.89	7.42	22.84
Limnichidae	0.67	60.50	2.12	1.90	7.20	30.04
Oligochaeta	31.67	5.00	1.17	1.20	3.96	34.00
Pyraustidae	0.00	2.33	1.11	2.15	3.78	37.78
Nematoda	0.17	2.67	1.06	1.63	3.61	41.39
Teloganodidae	57.83	13.33	1.06	1.46	3.58	44.97
Leptoceridae	0.33	4.67	1.04	1.35	3.55	48.52
EL and RI = 29.92 %	EL	RI				
Leptoceridae	0.33	18.17	2.42	3.56	8.08	8.08
Philopotamidae	28.33	0.67	2.26	2.14	7.56	15.64
Baetidae	454.17	84.50	2.11	2.56	7.04	22.68
Hydropsychidae (L+P)	64.00	2.33	2.04	2.54	6.82	29.50
Heptageniidae	12.67	0.17	1.95	1.90	6.53	36.03
Teloganodidae	57.83	3.83	1.95	2.12	6.52	42.56
Helodidae	2.00	9.50	1.32	1.41	4.41	46.97
MO and RI = 38.05 %	MO	RI				
Simuliidae (L+P)	1348.83	31.50	4.02	1.94	10.57	10.57
Hydropsychidae (L+P)	141.67	2.33	2.50	4.92	6.57	17.14
Leptophlebiidae	375.33	30.83	2.39	1.53	6.28	23.42
Limnichidae	60.50	0.83	2.09	1.87	5.50	28.92
Baetidae	569.00	84.50	2.09	3.84	5.48	34.40
Philopotamidae	30.33	0.67	2.04	2.66	5.36	39.77
Heptageniidae	6.67	0.17	1.60	3.27	4.20	43.96
Oligochaeta	5.00	69.67	1.59	1.32	4.18	48.14
EL and ZA = 41.21 %	EL	ZA				
Baetidae	454.17	16.17	3.94	3.22	9.55	9.55
Philopotamidae	28.33	1.67	2.25	1.74	5.45	15.01
Athericidae	6.67	0.00	2.22	4.54	5.39	20.40
Heptageniidae	12.67	0.17	2.12	1.88	5.13	25.53
Hydropsychidae (L+P)	64.00	8.83	2.03	1.48	4.93	30.46
Leptophlebiidae	33.33	5.67	1.85	1.29	4.49	34.96
Chironomidae (L+P)	445.00	152.50	1.78	1.70	4.32	39.27
Notonemouridae	1.33	35.00	1.65	1.56	4.00	43.28
Acarina	25.50	5.50	1.56	1.35	3.78	47.05
MO and ZA = 50.85 %	MO	ZA				
Simuliidae (L+P)	1348.83	8.00	5.61	2.09	11.04	11.04
Leptophlebiidae	375.33	5.67	3.66	2.25	7.19	18.23
Baetidae	569.00	16.17	3.62	4.21	7.11	25.34
Limnichidae	60.50	0.00	2.64	1.96	5.18	30.53
Hydropsychidae (L+P)	141.67	8.83	2.48	2.20	4.88	35.41
Notonemouridae	0.33	35.00	2.14	2.04	4.21	39.63
Chironomidae (L+P)	702.50	152.50	2.14	2.11	4.21	43.83
Philopotamidae	30.33	1.67	2.01	2.09	3.95	47.79

Appendix 2.3 Continued.

$\overline{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\overline{\delta}_i$ %
RI and ZA = 40.08 %	RI	ZA				
Leptoceridae	18.17	0.33	2.79	3.10	6.97	6.97
Chironomidae (L+P)	585.83	152.50	2.35	2.10	5.87	12.84
Athericidae	6.00	0.00	2.35	7.77	5.87	18.71
Leptophlebiidae	30.83	5.67	2.05	1.42	5.10	23.81
Hydraenidae	4.17	56.50	2.00	1.27	4.99	28.80
Simuliidae (L+P)	31.50	8.00	1.75	1.40	4.36	33.16
Baetidae	84.50	16.17	1.74	1.66	4.34	37.50
Elmidae (L)	63.00	17.50	1.66	1.87	4.14	41.63
Acarina	19.00	5.50	1.48	1.28	3.70	45.33
Helodidae	9.50	2.67	1.35	1.26	3.36	48.69
EL and DU = 36.79 %	EL	DU				
Philopotamidae	28.33	0.00	3.01	4.55	8.19	8.19
Baetidae	454.17	32.83	2.99	3.96	8.13	16.32
Hydropsychidae (L+P)	64.00	1.50	2.63	2.29	7.14	23.46
Simuliidae (L+P)	16.17	179.33	2.39	1.41	6.50	29.96
Heptageniidae	12.67	0.00	2.16	1.98	5.87	35.83
Leptophlebiidae	33.33	2.00	2.06	1.54	5.60	41.43
Hydroptilidae (L+P)	0.83	10.50	1.64	1.63	4.46	45.89
MO and DU = 41.31 %	MO	DU				
Leptophlebiidae	375.33	2.00	3.87	2.85	9.36	9.36
Simuliidae (L+P)	1348.83	179.33	3.16	1.34	7.65	17.01
Hydropsychidae (L+P)	141.67	1.50	3.01	3.52	7.28	24.29
Baetidae	569.00	32.83	2.84	6.86	6.87	31.16
Philopotamidae	30.33	0.00	2.68	8.38	6.49	37.65
Limnichidae	60.50	1.67	1.95	1.87	4.73	42.38
Heptageniidae	6.67	0.00	1.84	6.78	4.44	46.82
RI and DU = 28.17 %	RI	DU				
Leptophlebiidae	30.83	2.00	2.19	1.66	7.78	7.78
Simuliidae (L+P)	31.50	179.33	1.92	1.48	6.81	14.59
Oligochaeta	69.67	19.00	1.66	1.21	5.91	20.50
Hydroptilidae (L+P)	1.17	10.50	1.47	1.50	5.24	25.74
Caenidae	0.00	11.17	1.25	0.86	4.44	30.18
Hydraenidae	4.17	12.50	1.24	1.08	4.41	34.59
Leptoceridae	18.17	5.17	1.13	1.22	4.03	38.61
Helodidae	9.50	1.67	0.99	1.15	3.51	42.13
Teloganodidae	3.83	12.67	0.96	1.23	3.42	45.54
Limnichidae	0.83	1.67	0.94	1.16	3.34	48.88
ZA and DU = 41.13 %	ZA	DU				
Simuliidae (L+P)	8.00	179.33	3.22	1.43	7.84	7.84
Chironomidae (L+P)	152.50	641.33	2.56	2.14	6.22	14.05
Athericidae	0.00	9.33	2.55	4.97	6.19	20.24
Hydroptilidae (L+P)	0.67	10.50	1.94	1.52	4.72	24.96
Ceratopogonidae	2.50	0.00	1.93	4.28	4.69	29.64
Leptoceridae	0.33	5.17	1.81	1.66	4.40	34.04
Oligochaeta	82.67	19.00	1.79	1.14	4.36	38.41
Caenidae	0.67	11.17	1.39	1.00	3.38	41.79
Hydropsychidae (L+P)	8.83	1.50	1.38	1.43	3.34	45.14
Leptophlebiidae	5.67	2.00	1.37	1.28	3.33	48.46
EL and LA = 40.96 %	EL	LA				
Baetidae	454.17	38.83	3.17	2.87	7.73	7.73
Heptageniidae	12.67	0.00	2.33	1.96	5.68	13.41
Chironomidae (L+P)	445.00	91.17	2.26	2.26	5.52	18.93
Athericidae	6.67	0.00	2.25	4.71	5.50	24.42
Hydropsychidae (L+P)	64.00	4.00	2.25	1.74	5.50	29.92
Elmidae (L)	58.33	4.50	1.98	3.57	4.85	34.77
Acarina	25.50	2.00	1.97	1.61	4.81	39.58
Teloganodidae	57.83	4.83	1.89	2.24	4.61	44.18
Helodidae	2.00	9.50	1.52	1.37	3.72	47.91

Appendix 2.3 Continued.

$\overline{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\,\overline{\delta}_i$ %
MO and LA = 50.03 %	MO	LA				
Simuliidae (L+P)	1348.83	43.67	4.13	1.79	8.26	8.26
Baetidae	569.00	38.83	2.97	3.97	5.93	14.19
Hydropsychidae (L+P)	141.67	4.00	2.71	2.76	5.42	19.60
Limnichidae	60.50	0.00	2.67	1.97	5.33	24.93
Chironomidae (L+P)	702.50	91.17	2.59	2.87	5.18	30.11
Leptophlebiidae	375.33	17.00	2.55	1.98	5.10	35.21
Hydraenidae	46.00	1.17	2.06	1.83	4.11	39.32
Athericidae	11.00	0.00	2.01	5.11	4.01	43.33
Heptageniidae	6.67	0.00	1.95	6.16	3.90	47.23
RI and LA = 36.80 %	RI	LA				
Chironomidae (L+P)	585.83	91.17	2.90	2.92	7.89	7.89
Leptoceridae	18.17	0.17	2.81	4.28	7.62	15.51
Athericidae	6.00	0.00	2.38	8.78	6.48	21.99
Elmidae (L)	63.00	4.50	2.15	2.80	5.85	27.84
Acarina	19.00	2.00	1.94	1.60	5.26	33.10
Oligochaeta	69.67	21.83	1.44	1.38	3.92	37.03
Glossosomatidae	0.00	2.50	1.39	1.34	3.79	40.81
Leptophlebiidae	30.83	17.00	1.29	1.13	3.51	44.32
Hydraenidae	4.17	1.17	1.26	1.19	3.43	47.75
ZA and LA = 38.30 %	ZA	LA				
Hydraenidae	56.50	1.17	2.74	1.63	7.17	7.17
Simuliidae (L+P)	8.00	43.67	2.24	1.48	5.85	13.02
Leptophlebiidae	5.67	17.00	1.81	1.28	4.71	17.74
Helodidae	2.67	9.50	1.68	1.37	4.37	22.11
Ecnomidae	2.67	0.17	1.59	1.64	4.15	26.26
Glossosomatidae	0.00	2.50	1.53	1.32	4.00	30.26
Oligochaeta	82.67	21.83	1.51	1.30	3.95	34.21
Nematoda	1.00	0.00	1.45	2.07	3.79	38.00
Hydroptilidae (L+P)	0.67	2.33	1.31	1.19	3.42	41.42
Acarina	5.50	2.00	1.30	1.17	3.38	44.81
Corydalidae	0.00	1.17	1.27	1.32	3.31	48.12
DU and LA = 40.82 %	DU	LA				
Chironomidae (L+P)	641.33	91.17	3.12	2.88	7.64	7.64
Athericidae	9.33	0.00	2.58	5.23	6.32	13.96
Leptophlebiidae	2.00	17.00	2.05	1.63	5.02	18.99
Simuliidae (L+P)	179.33	43.67	2.02	1.50	4.95	23.94
Philopotamidae	0.00	2.33	1.93	4.57	4.72	28.66
Leptoceridae	5.17	0.17	1.80	1.80	4.42	33.08
Hydraenidae	12.50	1.17	1.70	1.28	4.17	37.25
Acarina	13.00	2.00	1.56	1.29	3.83	41.08
Hydroptilidae (L+P)	10.50	2.33	1.46	1.27	3.58	44.65
Glossosomatidae	0.00	2.50	1.43	1.34	3.49	48.15
EL and BA = 44.36 %	EL	BA				
Baetidae	454.17	17.33	3.93	3.22	8.87	8.87
Hydropsychidae (L+P)	64.00	1.50	3.26	2.29	7.34	16.21
Philopotamidae	28.33	0.17	2.91	3.04	6.56	22.77
Chironomidae (L+P)	445.00	63.67	2.55	2.69	5.74	28.51
Heptageniidae	12.67	0.00	2.24	1.95	5.05	33.56
Acarina	25.50	1.67	2.22	1.70	5.02	38.58
Helodidae	2.00	38.17	2.17	1.75	4.90	43.48
Notonemouridae	1.33	41.33	2.14	2.12	4.82	48.30
MO and BA = 52.94 %	MO	BA				
Simuliidae (L+P)	1348.83	7.33	5.69	2.12	10.74	10.74
Baetidae	569.00	17.33	3.62	4.14	6.84	17.58
Hydropsychidae (L+P)	141.67	1.50	3.54	3.14	6.69	24.27
Chironomidae (L+P)	702.50	63.67	2.82	3.26	5.33	29.61
Philopotamidae	30.33	0.17	2.58	4.01	4.87	34.47
Notonemouridae	0.33	41.33	2.57	2.50	4.86	39.34
Limnichidae	60.50	0.50	2.21	2.05	4.17	43.50
Acarina	29.83	1.67	2.01	1.85	3.80	47.30

Appendix 2.3 Continued.

$\overline{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\overline{\delta}_i$ %
RI and BA = 38.69 %	RI	BA				
Chironomidae (L+P)	585.83	63.67	3.18	3.39	8.22	8.22
Teloganodidae	3.83	82.33	2.45	2.14	6.34	14.56
Acarina	19.00	1.67	2.21	1.69	5.70	20.26
Athericidae	6.00	0.17	2.03	3.27	5.25	25.51
Oligochaeta	69.67	14.83	1.92	1.28	4.97	30.48
Simuliidae (L+P)	31.50	7.33	1.90	1.30	4.91	35.39
Baetidae	84.50	17.33	1.82	1.78	4.71	40.10
Notonemouridae	4.50	41.33	1.73	1.85	4.47	44.56
Hydropsychidae (L+P)	2.33	1.50	1.38	1.78	3.56	48.12
ZA and BA = 38.25 %	ZA	BA				
Leptophlebiidae	5.67	36.00	2.38	1.49	6.22	6.22
Helodidae	2.67	38.17	2.34	1.61	6.13	12.35
Oligochaeta	82.67	14.83	2.05	1.12	5.37	17.72
Teloganodidae	15.33	82.33	1.85	1.35	4.83	22.54
Hydropsychidae (L+P)	8.83	1.50	1.84	1.48	4.80	27.35
Elmidae (L)	17.50	86.17	1.77	1.61	4.63	31.97
Leptoceridae	0.33	3.17	1.65	1.65	4.31	36.28
Simuliidae (L+P)	8.00	7.33	1.51	1.31	3.96	40.24
Elmidae (A)	4.67	3.83	1.47	1.38	3.84	44.07
Acarina	5.50	1.67	1.43	1.25	3.75	47.82
DU and BA = 42.79 %	DU	BA				
Chironomidae (L+P)	641.33	63.67	3.39	3.34	7.93	7.93
Simuliidae (L+P)	179.33	7.33	3.38	1.47	7.89	15.82
Leptophlebiidae	2.00	36.00	2.70	2.10	6.30	22.12
Athericidae	9.33	0.17	2.21	2.94	5.17	27.30
Teloganodidae	12.67	82.33	1.97	1.62	4.61	31.91
Helodidae	1.67	38.17	1.97	1.77	4.60	36.51
Acarina	13.00	1.67	1.85	1.44	4.33	40.84
Hydroptilidae (L+P)	10.50	0.83	1.80	1.54	4.20	45.04
Ecnomidae	1.00	4.83	1.71	1.66	3.99	49.03
LA and BA = 41.77 %	LA	BA				
Teloganodidae	4.83	82.33	2.44	2.08	5.85	5.85
Simuliidae (L+P)	43.67	7.33	2.40	1.39	5.76	11.61
Ecnomidae	0.17	4.83	2.21	2.30	5.28	16.89
Elmidae (L)	4.50	86.17	2.18	1.95	5.23	22.12
Philopotamidae	2.33	0.17	1.77	2.17	4.24	26.35
Hydraenidae	1.17	7.83	1.73	1.48	4.15	30.51
Leptoceridae	0.17	3.17	1.64	1.78	3.92	34.42
Hydropsychidae (L+P)	4.00	1.50	1.59	1.32	3.81	38.23
Helodidae	9.50	38.17	1.49	1.04	3.57	41.81
Glossosomatidae	2.50	0.00	1.49	1.33	3.56	45.37
Oligochaeta	21.83	14.83	1.44	1.10	3.45	48.82
EL and HE = 47.26 %	EL	HE				
Tricorythidae	0.00	248.00	5.93	6.44	12.54	12.54
Teloganodidae	57.83	0.00	4.15	5.56	8.79	21.33
Elmidae (L)	58.33	1.33	3.50	3.51	7.42	28.74
Philopotamidae	28.33	0.00	3.41	4.54	7.21	35.96
Athericidae	6.67	0.00	2.36	5.00	5.00	40.96
Oligochaeta	31.67	18.67	2.31	1.45	4.89	45.85
MO and HE = 52.35 %	MO	HE				
Simuliidae (L+P)	1348.83	18.67	5.98	1.95	11.42	11.42
Tricorythidae	0.00	248.00	4.96	5.00	9.47	20.89
Philopotamidae	30.33	0.00	2.97	7.98	5.68	26.58
Hydraenidae	46.00	0.00	2.87	4.09	5.48	32.06
Limnichidae	60.50	0.00	2.78	1.99	5.30	37.36
Leptophlebiidae	375.33	123.33	2.54	1.41	4.85	42.21
Teloganodidae	13.33	0.00	2.27	5.05	4.35	46.55

Appendix 2.3 Continued.

$\overline{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\overline{\delta}_i$ %
RI and HE = 56.24 %	RI	HE				
Tricorythidae	0.00	248.00	6.23	5.69	11.08	11.08
Heptageniidae	0.17	94.67	4.56	3.35	8.11	19.18
Elmidae (L)	63.00	1.33	3.76	3.09	6.68	25.87
Leptoceridae	18.17	0.00	3.26	8.81	5.79	31.66
Hydropsychidae (L+P)	2.33	100.67	3.12	4.44	5.54	37.20
Oligochaeta	69.67	18.67	2.88	1.53	5.12	42.32
Helodidae	9.50	0.00	2.56	4.25	4.55	46.87
ZA and HE = 60.44 %	ZA	HE				
Tricorythidae	1.83	248.00	5.64	4.06	9.33	9.33
Heptageniidae	0.17	94.67	5.05	3.14	8.35	17.67
Baetidae	16.17	280.67	4.04	2.86	6.68	24.36
Hydraenidae	56.50	0.00	3.92	3.79	6.49	30.84
Notonemouridae	35.00	0.00	3.64	3.93	6.02	36.86
Oligochaeta	82.67	18.67	3.34	1.60	5.53	42.39
Leptophlebiidae	5.67	123.33	3.29	1.40	5.45	47.84
DU and HE = 61.62 %	DU	HE				
Tricorythidae	0.00	248.00	6.39	5.91	10.37	10.37
Heptageniidae	0.00	94.67	4.99	3.79	8.09	18.46
Hydropsychidae (L+P)	1.50	100.67	3.86	3.20	6.26	24.72
Simuliidae (L+P)	179.33	18.67	3.73	1.47	6.05	30.77
Leptophlebiidae	2.00	123.33	3.36	1.52	5.45	36.22
Baetidae	32.83	280.67	2.85	4.03	4.62	40.84
Elmidae (L)	27.17	1.33	2.84	2.45	4.61	45.46
Athericidae	9.33	0.00	2.72	5.75	4.41	49.87
LA and HE = 58.29 %	LA	HE				
Tricorythidae	0.00	248.00	7.00	5.21	12.02	12.02
Heptageniidae	0.00	94.67	5.47	3.52	9.39	21.40
Hydropsychidae (L+P)	4.00	100.67	3.52	2.38	6.04	27.44
Notonemouridae	10.33	0.00	3.18	8.20	5.46	32.90
Baetidae	38.83	280.67	3.08	2.51	5.28	38.18
Simuliidae (L+P)	43.67	18.67	2.73	1.32	4.68	42.86
Helodidae	9.50	0.00	2.68	2.14	4.59	47.46
BA and HE = 68.36 %	BA	HE				
Tricorythidae	0.00	248.00	6.69	5.11	9.78	9.78
Heptageniidae	0.00	94.67	5.22	3.51	7.64	17.42
Teloganodidae	82.33	0.00	5.04	4.07	7.37	24.79
Hydropsychidae (L+P)	1.50	100.67	4.71	2.80	6.89	31.68
Notonemouridae	41.33	0.00	4.26	3.97	6.24	37.92
Baetidae	17.33	280.67	4.02	2.86	5.89	43.80
Helodidae	38.17	0.00	3.90	5.57	5.70	49.51

Appendix 2.4 **Select descriptors of riffle physical habitat for the eight sites (*n* = 6 replicate samples per site).** Means (± SD), minima and maxima are presented for each variable. Data for the two locations within each site were grouped, as no significant differences in physical habitat conditions were found between each pair. Median (d_{50}), minimum (min) and maximum (max) values are provided for the dominant (DOM) and subdominant (SUBDOM) substratum (SUBSTR) particle size. OTHER denotes the surface substratum remaining after the DOM and SUBDOM components have been accounted for. Descriptors of subsurface substratum composition are also provided. MBBS - minimum bottom shear stress; MI - microprofile index; CV - coefficient of variation.

SITE	DU TOITS			MOLENAARS			ELANDS			HEX		
VARIABLE	**Mean (± SD)**	**Min**	**Max**	**Mean (± SD)**	**Min**	**Max**	**Mean (± SD)**	**Min**	**Max**	**Mean (± SD)**	**Min**	**Max**
Depth (m)	0.15 (± 0.03)	0.13	0.20	0.12 (± 0.05)	0.06	0.17	0.13 (± 0.05)	0.07	0.20	0.11 (± 0.05)	0.07	0.18
Average velocity (m^3 s^{-1})	0.565 (± 0.357)	0.206	1.023	0.680 (± 0.209)	0.495	0.973	0.588 (± 0.498)	0.103	1.503	0.363 (± 0.139)	0.127	0.528
Near-bottom velocity (m^3 s^{-1})	0.509 (± 0.372)	0.108	0.976	0.691 (± 0.227)	0.459	0.966	0.541 (± 0.661)	0.055	1.775	0.358 (± 0.155)	0.061	0.498
Froude No.	0.470 (± 0.300)	0.182	0.873	0.701 (± 0.359)	0.442	1.268	0.591 (± 0.626)	0.104	1.813	0.361 (± 0.138)	0.102	0.499
MBSS (dyn cm^{-2})	13.43 (± 17.27)	1.66	44.80	45.69 (± 36.79)	2.72	89.50	14.87 (± 10.96)	2.72	31.70	20.74 (± 34.02)	1.66	89.50
Instream cover (%)	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0
Overhead cover (%)	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0
DOM SUBSTR area (%)	58.3 (± 11.7)	40.0	70.0	46.7 (± 18.6)	20.0	70.0	73.3 (± 17.5)	50.0	100.0	63.3 (± 23.8)	35.0	100.0
DOM SUBSTR d_{50} (mm)	191.3 (± 72.9)	85.0	275.0	206.2 (± 106.3)	90.0	355.0	174.5 (± 59.0)	115.0	255.0	173.3 (± 68.8)	70.0	270.0
DOM SUBSTR min (mm)	153.7 (± 64.5)	75.0	240.0	138.7 (± 55.4)	55.0	200.0	129.8 (± 40.6)	80.0	190.0	114.7 (± 39.4)	42.0	160.0
DOM SUBSTR max (mm)	228.3 (± 88.1)	105.0	330.0	548.3 (± 285.9)	270.0	1090.0	395.3 (± 223.1)	175.0	790.0	310.0 (± 131.9)	140.0	535.0
DOM SUBSTR no. of particles	5.2 (± 4.9)	2.0	15.0	5.3 (± 3.4)	3.0	12.0	5.0 (± 1.3)	3.0	6.0	6.0 (± 5.4)	3.0	17.0
SUBDOM SUBSTR area (%)	30.8 (± 4.9)	25.0	40.0	44.2 (± 17.4)	25.0	70.0	26.7 (± 17.5)	0.0	50.0	35.0 (± 22.6)	0.0	65.0
SUBDOM SUBSTR d_{50} (mm)	67.9 (± 42.0)	35.0	150.0	60.8 (± 19.2)	24.5	80.0	33.8 (± 23.8)	0.0	67.5	40.3 (± 26.0)	0.0	72.0
SUBDOM SUBSTR min (mm)	55.5 (± 37.0)	30.0	130.0	40.3 (± 16.7)	15.0	60.0	26.2 (± 24.6)	0.0	65.0	24.8 (± 15.5)	0.0	42.0
SUBDOM SUBSTR max (mm)	86.8 (± 47.4)	40.0	160.0	96.7 (± 30.9)	60.0	145.0	51.3 (± 29.3)	0.0	80.0	70.5 (± 37.1)	0.0	110.0
SUBDOM SUBSTR no. of particles	3.7 (± 1.2)	2.0	5.0	16.2 (± 19.0)	3.0	54.0	23.5 (± 40.3)	0.0	105.0	10.3 (± 7.2)	0.0	17.0
OTHER SUBSTR area (%)	0.0 (± 0.0)	0.0	0.0	9.2 (± 9.2)	0.0	25.0	0.0 (± 0.0)	0.0	0.0	2.5 (± 4.2)	0.0	10.0
OTHER d_{50} (mm)	0.0 (± 0.0)	0.0	0.0	14.1 (± 15.2)	0.0	30.0	0.0 (± 0.0)	0.0	0.0	6.2 (± 9.7)	0.0	21.0
Subsurface area (%)	13.3 (± 7.5)	5.0	25.0	100.0 (± 0.0)	100.0	100.0	83.3 (± 40.8)	0.0	100.0	83.3 (± 25.8)	50.0	100.0
Subsurface d_{50} (mm)	24.8 (± 4.5)	19.0	30.0	47.4 (± 27.1)	20.0	80.0	18.2 (± 10.3)	0.0	31.0	32.1 (± 21.7)	13.5	72.0
Subsurface min (mm)	21.0 (± 6.6)	12.0	30.0	28.2 (± 22.7)	4.0	60.0	9.0 (± 5.5)	0.0	15.0	17.0 (± 17.7)	0.1	42.0
Subsurface max (mm)	27.0 (± 7.3)	19.0	40.0	82.2 (± 44.3)	30.0	145.0	25.5 (± 15.0)	0.0	41.0	48.3 (± 31.3)	22.0	110.0
No. of SUBSTR layers	1.1 (± 0.1)	1.0	1.3	2.0 (± 0.0)	2.0	2.0	1.6 (± 0.3)	1.0	1.8	1.6 (± 0.2)	1.5	2.0
SUBSTR embeddedness (%)	0.0 (± 0.0)	0.0	0.0	1.7 (± 4.1)	0.0	10.0	0.8 (± 2.0)	0.0	5.0	3.3 (± 4.1)	0.0	10.0
SUBSTR compaction (range)	moderate-high			very low-high			very low-very high			very low-very high		
SUBSTR shape (range)	subangular			subround			subround			subround		
SUBSTR MI (mm)	32.0 (± 10.6)	15.5	46.4	47.1 (± 7.5)	39.2	61.1	45.1 (± 20.2)	23.8	78.6	35.8 (± 10.5)	22.9	53.7
SUBSTR MI CV	0.4 (± 0.2)	0.2	0.7	0.7 (± 0.3)	0.3	1.1	0.6 (± 0.3)	0.2	0.9	0.4 (± 0.2)	0.2	0.7

Appendix 2.4 Continued.

VARIABLE	ZACHARIASHOEK			LANGRIVIER			RIVIERSONDEREND			BAKKERSKLOOF		
	Mean (± SD)	Min	Max	Mean (± SD)	Min	Max	Mean (± SD)	Min	Max	Mean (± SD)	Min	Max
Depth (m)	0.05 (± 0.02)	0.03	0.10	0.07 (± 0.01)	0.05	0.09	0.10 (± 0.04)	0.05	0.16	0.05 (± 0.02)	0.03	0.08
Average velocity (m^3 s^{-1})	0.324 (± 0.235)	0.146	0.694	0.524 (± 0.317)	0.202	1.061	0.525 (± 0.224)	0.273	0.848	0.183 (± 0.128)	0.088	0.439
Near-bottom velocity (m^3 s^{-1})	0.316 (± 0.238)	0.134	0.684	0.469 (± 0.291)	0.220	0.955	0.520 (± 0.263)	0.128	0.803	0.175 (± 0.132)	0.088	0.439
Froude No.	0.498 (± 0.392)	0.179	1.010	0.634 (± 0.405)	0.244	1.280	0.592 (± 0.369)	0.276	1.105	0.283 (± 0.212)	0.115	0.701
MBSS (dyn cm^{-2})	3.88 (± 3.04)	0.95	8.26	11.92 (± 16.32)	2.18	44.8	6.56 (± 1.70)	3.93	8.26	1.76 (± 1.10)	0.95	3.93
Instream cover (%)	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0	0.0 (± 0.0)	0.0	0.0	0.8 (± 2.0)	0.0	5.0
Overhead cover (%)	2.5 (± 2.7)	0.0	5.0	75.0 (± 0.0)	75.0	75.0	0.0 (± 0.0)	0.0	0.0	1.7 (± 2.6)	0.0	5.0
DOM SUBSTR area (%)	45.8 (± 9.2)	35.0	60.0	54.2 (± 18.0)	20.0	70.0	47.5 (± 15.4)	30.0	70.0	42.5 (± 16.0)	20.0	65.0
DOM SUBSTR d_{50} (mm)	113.4 (± 27.3)	83.0	158.5	211.9 (± 53.6)	154.0	289.0	182.4 (± 33.9)	160.0	250.0	177.9 (± 40.9)	135.0	230.0
DOM SUBSTR min (mm)	92.5 (± 34.5)	64.0	155.0	163.5 (± 68.3)	105.0	287.0	116.8 (± 9.9)	103.0	132.0	152.2 (± 46.2)	93.0	210.0
DOM SUBSTR max (mm)	189.7 (± 46.2)	141.0	245.0	305.8 (± 113.5)	175.0	465.0	307.8 (± 117.3)	210.0	530.0	261.7 (± 63.8)	152.0	330.0
DOM SUBSTR no. of particles	4.2 (± 1.6)	2.0	6.0	3.7 (± 1.2)	2.0	5.0	4.2 (± 1.2)	3.0	6.0	3.8 (± 1.0)	3.0	5.0
SUBDOM SUBSTR area (%)	42.5 (± 9.9)	30.0	50.0	41.7 (± 15.1)	30.0	70.0	44.2 (± 13.6)	30.0	65.0	39.2 (± 13.9)	25.0	65.0
SUBDOM SUBSTR d_{50} (mm)	41.1 (± 14.3)	29.0	64.0	34.7 (± 27.1)	16.0	86.5	44.8 (± 16.0)	22.5	64.0	51.8 (± 18.1)	22.0	71.0
SUBDOM SUBSTR min (mm)	23.3 (± 18.3)	5.0	58.0	9.3 (± 9.1)	3.0	22.0	19.5 (± 11.3)	4.0	32.0	25.7 (± 12.4)	7.0	41.0
SUBDOM SUBSTR max (mm)	81.0 (± 15.4)	68.0	100.0	113.3 (± 40.3)	77.0	185.0	95.7 (± 17.2)	80.0	123.0	97.2 (± 25.1)	72.0	142.0
SUBDOM SUBSTR no. of particles	30.7 (± 31.7)	4.0	92.0	25.3 (± 28.9)	2.0	81.0	29.2 (± 21.2)	7.0	67.0	35.2 (± 58.8)	8.0	155.0
OTHER SUBSTR area (%)	11.7 (± 6.8)	0.0	20.0	4.2 (± 4.9)	0.0	10.0	8.3 (± 9.8)	0.0	20.0	18.3 (± 10.3)	0.0	30.0
OTHER d_{50} (mm)	6.7 (± 6.4)	0.0	15.0	9.2 (± 10.1)	0.0	20.0	14.3 (± 16.2)	0.0	36.0	8.9 (± 6.3)	0.0	18.0
Subsurface area (%)	46.7 (± 44.9)	0.0	100.0	58.3 (± 49.2)	0.0	100.0	75.0 (± 41.8)	0.0	100.0	0.0 (± 0.0)	0.0	0.0
Subsurface d_{50} (mm)	15.1 (± 11.1)	0.0	31.5	28.7 (± 32.6)	0.0	86.5	38.9 (± 24.4)	0.0	64.0	0.0 (± 0.0)	0.0	0.0
Subsurface min (mm)	3.9 (± 7.2)	0.0	18.0	8.0 (± 10.2)	0.0	22.0	17.3 (± 13.8)	0.0	32.0	0.0 (± 0.0)	0.0	0.0
Subsurface max (mm)	31.0 (± 23.4)	0.0	68.0	85.5 (± 73.9)	0.0	185.0	82.3 (± 43.2)	0.0	123.0	0.0 (± 0.0)	0.0	0.0
No. of SUBSTR layers	1.5 (± 0.5)	1.0	2.0	1.6 (± 0.5)	1.0	2.0	1.8 (± 0.4)	1.0	2.0	1.0 (± 0.0)	1.0	1.0
SUBSTR embeddedness (%)	5.0 (± 7.7)	0.0	20.0	0.8 (± 2.0)	0.0	5.0	0.8 (± 2.0)	0.0	5.0	14.2 (± 7.4)	5.0	20.0
SUBSTR compaction (range)	low-high			low-very high			very low-very high			very low-very high		
SUBSTR shape (range)	subangular-subround			subangular-subround			subround			subangular-subround		
SUBSTR MI (mm)	33.0 (± 14.2)	17.6	56.4	41.4 (± 15.9)	20.2	65.2	36.9 (± 5.0)	30.6	43.0	31.4 (± 8.2)	21.2	43.8
SUBSTR MI CV	0.3 (± 0.2)	0.1	0.7	0.5 (± 0.2)	0.2	0.7	0.4 (± 0.1)	0.3	0.5	0.3 (± 0.1)	0.2	0.5

Appendix 3.1 Summary of the types of data, number of samples collected and sampling dates, for all six sampling trips during the low flow study. Similar sets of data were collected for each of the two locations at each of the four sites, as indicated. BMIs – benthic macroinvertebrates. Each sample comprised three separate parts: T = top of stone; B = bottom of stone; U = underlying substratum. A subset of U sample parts from only riffles and runs was analysed, for Dec, Feb and Apr.

EXPERIMENTAL PHASE	ELANDS SITE			
TRIP NO.	CONTROL LOCATION		IMPACT LOCATION	
TYPE OF DATA	Sampling date(s)	No. of samples	Sampling date(s)	No. of samples
PRE-IMPACT PHASE				
TRIP 1 - DECEMBER				
BMIs	23/12/94; 27-28/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	21/12/94; 28/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	27/12/94	1 full set	27/12/94	1 full set
Biotope maps	14/12/94	1 set for 60 m	13/12/94	1 set for 60 m
Cross-sections	14-15/12/94	1 riffle; 1 run	13/12/94	1 riffle; 1 run
TRIP 2 - JANUARY				
BMIs	19/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	19/01/95; 24/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	24/01/95	1 full set	24/01/95	1 full set
Biotope maps	12/01/95	1 set for 60 m	12/01/95	1 set for 60 m
Cross-sections	12/01/95	1 riffle; 1 run	12/01/95	1 riffle; 1 run
IMPACT PHASE				
TRIP 3 - FEBRUARY/EARLY MARCH				
BMIs	19/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	27/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	28/02/95	1 full set	28/02/95	1 full set
Biotope maps	02/03/95	1 set for 60 m	03/03/95	1 set for 60 m
Cross-sections	02/03/95	1 riffle; 1 run	02-03/03/95	1 riffle; 1 run
TRIP 4 - MARCH				
BMIs	16-17/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	17/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	30/03/95	1 full set	30/03/95	1 full set
Biotope maps	27/03/95	1 set for 60 m	27/03/95	1 set for 60 m
Cross-sections	27/03/95	1 riffle; 1 run	27/03/95	1 riffle; 1 run
POST-IMPACT PHASE				
TRIP 5 - APRIL				
BMIs	10/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	24/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	10/04/95	1 full set	24/04/95	1 full set
Biotope maps	20/04/95	1 set for 60 m	20/04/95	1 set for 60 m
Cross-sections	20/04/95	1 riffle; 1 run	20/04/95	1 riffle; 1 run
TRIP 6 - MAY				
BMIs	07/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	10/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	01/05/95	1 full set	01/05/95	1 full set
Biotope maps	17/05/95	1 set for 60 m	17/05/95	1 set for 60 m
Cross-sections	17/05/95	1 riffle; 1 run	17/05/95	1 riffle; 1 run

Appendix 3.1 Continued.

EXPERIMENTAL PHASE	MOLENAARS SITE			
TRIP NO.	CONTROL LOCATION		IMPACT LOCATION	
TYPE OF DATA	Sampling date(s)	No. of samples	Sampling date(s)	No. of samples
PRE-IMPACT PHASE				
TRIP 1 - DECEMBER				
BMIs	18/12/94; 26-27/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	24-26/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	18/12/94	1 full set	18/12/94	1 full set
Biotope maps	20/12/94	1 set for 60 m	19/12/94	1 set for 60 m
Cross-sections	20/12/94	1 riffle; 1 run	19/12/94	1 riffle; 1 run
TRIP 2 - JANUARY				
BMIs	22-23/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	21-22/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat		As per BMIs		As per BMIs
Water chemistry	23/01/95	1 full set	23/01/95	1 full set
Biotope maps	17/01/95	1 set for 60 m	17/01/95	1 set for 60 m
Cross-sections	17/01/95	1 riffle; 1 run	17/01/95	1 riffle; 1 run
IMPACT PHASE				
TRIP 3 - FEBRUARY/EARLY MARCH				
BMIs	17/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	25/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat		As per BMIs		As per BMIs
Water chemistry	17/02/95	1 full set	24/02/95	1 full set
Biotope maps	07/03/95	1 set for 60 m	07/03/95	1 set for 60 m
Cross-sections	07/03/95	1 riffle; 1 run	07/03/95	1 riffle; 1 run
TRIP 4 - MARCH				
BMIs	15/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	22/03/95; 24/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat		As per BMIs		As per BMIs
Water chemistry	29/03/95	1 full set	29/03/95	1 full set
Biotope maps	28/03/95	1 set for 60 m	28/03/95	1 set for 60 m
Cross-sections	28/03/95	1 riffle; 1 run	28/03/95	1 riffle; 1 run
POST-IMPACT PHASE				
TRIP 5 - APRIL				
BMIs	11/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	13/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat		As per BMIs		As per BMIs
Water chemistry	11/04/95	1 full set	13/04/95	1 full set
Biotope maps	19/04/95	1 set for 60 m	19/04/95	1 set for 60 m
Cross-sections	19/04/95	1 riffle; 1 run	19/04/95	1 riffle; 1 run
TRIP 6 - MAY				
BMIs	09/05/95; 14/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	09/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	01/05/95	1 full set	01/05/95	1 full set
Biotope maps	16/05/95	1 set for 60 m	16/05/95	1 set for 60 m
Cross-sections	16/05/95	1 riffle; 1 run	16/05/95	1 riffle; 1 run

Appendix 3.1 Continued.

EXPERIMENTAL PHASE	DU TOITS SITE			
TRIP NO.	**CONTROL LOCATION**		**IMPACT LOCATION**	
TYPE OF DATA	**Sampling date(s)**	**No. of samples**	**Sampling date(s)**	**No. of samples**
PRE-IMPACT PHASE				
TRIP 1 - DECEMBER				
BMIs	18/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	10/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	10/12/94	1 full set	10/12/94	1 full set
Biotope maps	05-06/12/94	1 set for 60 m	05/12/94	1 set for 60 m
Cross-sections	06/12/94	1 riffle; 1 run	06/12/94	1 riffle; 1 run
TRIP 2 - JANUARY				
BMIs	16/01/95; 18/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	15-16/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	18/01/95	1 full set	18/01/95	1 full set
Biotope maps	11/01/95	1 set for 60 m	11/01/95	1 set for 60 m
Cross-sections	11/01/95	1 riffle; 1 run	11/01/95	1 riffle; 1 run
IMPACT PHASE				
TRIP 3 - FEBRUARY				
BMIs	15-16/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	20-21/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	16/02/95	1 full set	20/02/95	1 full set
Biotope maps	23-24/02/95	1 set for 60 m	23/02/95	1 set for 60 m
Cross-sections	24/02/95	1 riffle; 1 run	23/02/95	1 riffle; 1 run
TRIP 4 - MARCH				
BMIs	14/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	13/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	12/03/95	1 full set	12/03/95	1 full set
Biotope maps	21/03/95	1 set for 60 m	21/03/95	1 set for 60 m
Cross-sections	21/03/95	1 riffle; 1 run	21/03/95	1 riffle; 1 run
POST-IMPACT PHASE				
TRIP 5 - APRIL				
BMIs	09/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	14/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	09/04/95	1 full set	14/04/95	1 full set
Biotope maps	17/04/95	1 set for 60 m	17/04/95	1 set for 60 m
Cross-sections	17/04/95	1 riffle; 1 run	17/04/95	1 riffle; 1 run
TRIP 6 - MAY				
BMIs	08/05/95; 12/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	03/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	03/05/95	1 full set	03/05/95	1 full set
Biotope maps	12/05/95	1 set for 60 m	12/05/95	1 set for 60 m
Cross-sections	12/05/95	1 riffle; 1 run	12/05/95	1 riffle; 1 run

Appendix 3.1 Continued.

EXPERIMENTAL PHASE	RIVIERSONDEREND SITE			
TRIP NO.	CONTROL LOCATION		IMPACT LOCATION	
TYPE OF DATA	Sampling date(s)	No. of samples	Sampling date(s)	No. of samples
PRE-IMPACT PHASE				
TRIP 1 - DECEMBER				
BMIs	04/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	03-04/12/94; 10/12/94	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat	As per BMI	As per BMI	As per BMI	As per BMI
Water chemistry	03/12/94	1 full set	03/12/94	1 full set
Biotope maps	12/12/94	1 set for 60 m	07/12/94	1 set for 60 m
Cross-sections	12/12/94	1 riffle; 1 run	07/12/94	1 riffle; 1 run
TRIP 2 - JANUARY				
BMIs	09/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	13/01/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat		As per BMI		As per BMI
Water chemistry	13/01/95	1 full set	13/01/95	1 full set
Biotope maps	10/01/95	1 set for 60 m	10/01/95	1 set for 60 m
Cross-sections	10/01/95	1 riffle; 1 run	10/01/95	1 riffle; 1 run
IMPACT PHASE				
TRIP 3 - FEBRUARY				
BMIs	11-12/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	14-15/02/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat		As per BMI		As per BMI
Water chemistry	15/02/95	1 full set	15/02/95	1 full set
Biotope maps	22/02/95	1 set for 60 m	22/02/95	1 set for 60 m
Cross-sections	22/02/95	1 riffle; 1 run	22/02/95	1 riffle; 1 run
TRIP 4 - MARCH				
BMIs	10/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	10-11/03/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat		As per BMI		As per BMI
Water chemistry	12/03/95	1 full set	12/03/95	1 full set
Biotope maps	20/03/95	1 set for 60 m	20/03/95	1 set for 60 m
Cross-sections	20/03/95	1 riffle; 1 run	20/03/95	1 riffle; 1 run
POST-IMPACT PHASE				
TRIP 5 - APRIL				
BMIs	08/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B	22/04/95	• 3 riffle T+B+U • 3 run T+B+U • 3 pool T+B
Physical microhabitat		As per BMI		As per BMI
Water chemistry	08/04/95	1 full set	22/04/95	1 full set
Biotope maps	18/04/95	1 set for 60 m	18/04/95	1 set for 60 m
Cross-sections	18/04/95	1 riffle; 1 run	18/04/95	1 riffle; 1 run
TRIP 6 - MAY				
BMIs	04/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B	04-05/05/95; 13/05/95	• 3 riffle T+B • 3 run T+B • 3 pool T+B
Physical microhabitat	As per BMIs	As per BMIs	As per BMIs	As per BMIs
Water chemistry	04/05/95	1 full set	04/05/95	1 full set
Biotope maps	11/05/95	1 set for 60 m	11/05/95	1 set for 60 m
Cross-sections	11/05/95	1 riffle; 1 run	11/05/95	1 riffle; 1 run

Appendix 3.2 Explanation of the coding procedure used when field surveying the template for biotope mapping and the cross-sections at each site location (Section 3.4).

CODE	DESCRIPTION
EL	Elands site
MO	Molenaars site
DU	Du Toits site
RI	Riviersonderend site
C	Control location at site
I	Impact location at site
CM1, CM10, ..., CM60	Control location map, beacon indicating transect line at 1 m, 10 m, ..., 60 m
IM1 - IM60	Impact location map, beacon indicating transect line at 1 m, 10 m, ..., 60 m
IC5, IC15, ..., IC55	Control map, intermediate pegs indicating transects at 5 m, 15 m, ..., 55 m intervals
I5, I15, ..., I55	Impact map, intermediate pegs indicating transects at 5 m, 15 m, ..., 55 m intervals
BM	Survey benchmark(s) for the location
ELR1, ELL1, ...ELL4	For each site (e.g. EL), cross-section headstakes on right (R) and left (L) bank, for cross-sections 1 - 4; cross-sections 1 and 2 represent the control location, and cross-sections 3 and 4 represent the impact location
EW1, EW2, ..., EWn	Right bank and left bank water's edges (EW – edge of water) of the main channel, at all 10 m transects
WSE1, WSE2, ..., WSE5	Water surface elevations 1 - 5, for each cross-section
WSEM1, WSEM2, ..., WSEMn	Water surface elevations at each of the 10 m transect intervals, for each location
1.1, 1.2, ..., 1.n	Dry points (e.g. on the bank) or water's edge spotshots, in sequence across cross-section 1
2.1, 2.2, ..., 2.n	Dry points or water's edge spotshots, in sequence across cross-section 2
3.1, 3.2, ..., 3.n	Dry points or water's edge spotshots, in sequence across cross-section 3
4.1, 4.2, ..., 4.n	Dry point or water's edge spotshots, in sequence across cross-section 4
MA1, MA2, ..., MAn	Instream spotshots, in sequence across each cross-section; instream spotshots are linked with other point microhabitat data (depth, velocity, etc.) using float marker (MA) numbers

Appendix 3.2 Continued.

CODE	DESCRIPTION
0	General code for benchmark, beacon, headstake, WSE or EW spotshots
1	Bank
2	Water's edge of main river channel
3	Water's edge of secondary channel or wetted area
4	Water trickling between partially exposed substratum elements
5	Exposed or dry instream cobble/boulder bar
6	Run
7	Riffle, as a patch
8	Riffle, as a structured cobble/boulder bar
9	Pool, in-channel or marginal (including slackwaters, dead zones)
10	Pool-run transition
11	Riffle-run transition
12	Bedrock rapid (not encountered)
13	Location of temporary flow diversion weir
14	Exposed/dry boulder
15	Submerged boulder
16	Backwater pool
17	Undercut bank
18	*Prionium serratum*, instream or marginal
19	Bedrock outcrop on channel edge
20	Inflow from side stream or seep
21	Tree roots/branches/woody debris
22	Water's edge on exposed boulder/bedrock
23	*Isolepis digitata*, instream or marginal
24	Standing or stagnant water
25	Exposed/dry bedrock
26	Submerged bedrock
27	Drying side channel

Appendix 3.3 Descriptions of hydraulic biotope types visually identified in the field (adapted from King and Tharme 1994). Appendix 3.4 provides corresponding descriptions of and codes for flow types and substrata commonly associated with each biotope.

HYDRAULIC BIOTOPE	DESCRIPTION	ASSOCIATED FLOW TYPE(S)
Riffle	Typically shallow to moderately deep; low depth to substratum ratio; commonly fast flickering flow, with typically high velocities and visible turbulence, often but nor always, indicated by a broken water surface; substratum variable but typically coarse alluvium (gravel to boulders), predominantly small cobble to small boulders, little deposition of fines such as sand or silt, low embeddedness of substratum elements in surrounding bed materials, variable bed compactness, but often some highly compact (immovable) elements; overall feature represents an elevated area of deposited coarse sediment in the long profile of the undulating bed, generally noticeable change in bed slope from riffle head to foot, either gradually ("slope riffle") or distinctly ("bar riffle"), forming elevated cobble/boulder bars where some flow may be funnelled between macro bed elements (i.e. chute biotope); erosive environment; hydraulic migration upstream or downstream, or transformation to other biotopes, can occur with changes in discharge; may act as an hydraulic control affecting upstream and downstream flow conditions.	Predominantly BSW, USW, FRF, SRF; may include BOIL, CH and chaotic flow types, to a limited extent.
Riffle-run transition	Similar physical character to a riffle or run over cobbles/boulders, with high velocity water forming a deeply rippled or mostly undular surface, but without a broken water surface and with fairly low turbulence; typically moderate depth; patches adjoining either riffle or run biotopes; difficult to make an instantaneous visual classification as either riffle or run; potentially of transitional hydraulic character.	Predominantly USW and RS; may include FRF and SBT.
Run	Characterised by tranquil, smooth flow with velocity sufficient to cause some surface disruption in the form of ripples, but without a turbulent, clearly broken water surface; slow to high velocity water, fast runs may be differentiated from slow runs by the degree of ripple development, with fast runs possessing clear rippling and slow runs having indistinct ripples; variable water depth, where deep, moderate and shallow runs may be differentiated; typically high depth to substratum ratio; occurring over any substratum except silt, often over gravel, small or large cobbles and/or boulders; low to high embeddedness of substratum elements in surrounding bed materials, variable bed compactness; often located between pools and riffles or rapids; no apparent change in river bed slope or a limited slope along the length of the run; hydraulic migration upstream or downstream or transformation to other biotopes can occur with changes in discharge.	Predominantly SBT and RS; may include BPF, USW and SRF flow types, to a limited extent.
Pool-run transition	Possessing similar physical character to a slow run or flowing pool; difficult to make an instantaneous visual classification as either run or pool without measuring velocity in particular; potentially of transitional hydraulic character.	Predominantly BPF; may include SBT and NF.
Pool	Water depth variable from shallow to deep; slow-flowing, low velocity areas with little or no disruption of the water surface (except possibly at the head or foot of the pool), dominated by barely perceptible flow; no turbulence; variable substrata, ranging from bedrock to sand or silt, accumulation of fine sediment is often promoted by the characteristically low velocities (sometimes in association with deep water or channel margins); substratum elements often moderate to highly embedded in fines; usually in hydraulic contact with upstream and downstream water, but may become partially to entirely isolated from the main channel at low discharges, as standing bodies of water with zero velocity, due to a loss of connectivity of wetted area (i.e. 'partially/fully isolated pools'); typically occur between riffle or run units, either mid-channel or along the channel margins; often represented by low points within the long profile of the undulating bed; at high flows, scouring action and eddy effects can occur and pools may transform to other biotopes; depositional environments.	Typically represented by NF and BPF flow types; may also include the SBT flow type.
Backwater	Morphologically hydraulically detached section of channel occurring alongside but physically separated from the main channel, though connected to it at its downstream end; typically no through-flow and water enters in an upstream direction; depth variable; velocity tends to be low, often zero; occurs over a wide range of substratum types, though often dominated by gravel, cobbles, with deposition of fine material (e.g. sand, silt, organic detritus); depositional environments; may transform to other biotopes with changing flow.	Typically represented by NF and BPF flow types; may include SBT and RS flow types, to a limited extent.

Appendix 3.3 Continued.

HYDRAULIC BIOTOPE	DESCRIPTION	ASSOCIATED FLOW TYPE(S)
Trickle run	Patches of moderately slow to very slow, very shallow flow, where the flow is among and not submerging the majority of substratum elements (i.e. majority of bed elements at least partially exposed); substratum may comprise any combination of size classes, but commonly includes gravel, small to large cobbles or small boulders, and may have accumulations of detritus; often located between pools and runs, along channel margins; may transform to other biotopes with changes in flow.	Represented entirely by the TR flow type.
Standing water	Typically small to moderately-sized patches of non-flowing water, commonly very shallow, entirely separated from the flowing channel by exposed substratum areas; differentiated from isolated pools in that they do not represent main channel pools that have become isolated through flow reduction, and are relatively smaller and shallower; may transform to other biotopes with flow change.	Represented entirely by the NF flow type.

Appendix 3.4 Categories of visually distinct flow types and substrata commonly used in field-based identification of hydraulic biotopes (from King and Schael 2001 - based on descriptions in Rowntree 1996; Padmore 1998; Wadeson and Rowntree 1998; Newson *et al.* 1998). Chaotic flow, cascade, chute, stream, fast and slow riffle, and trickle flow types were not recognised by all authors.

CATEGORY	DESCRIPTION
FLOW TYPE (code)	DEFINITION
Free falling (FF)	Water falls vertically without obstruction.
Cascade (CAS)	Water tumbling down a stepped series of boulders, large cobble or bedrock.
Boil (BOIL)	Water forming bubbles, as in rapidly boiling water, usually below a waterfall or strong chute; boil forms on the water surface; direction of flow is predominantly vertical, with strong horizontal eddies.
Chute (CH)	Water forced between two rocks, usually large cobble or boulders; flowing fast with the fall too low to be considered free falling.
Stream (STR)	Water flowing rapidly in a smooth sheet of water; similar to a chute but not forced between two bed elements.
Broken standing waves (BSW)	Standing waves are present which break at the crest (white water).
Undular standing waves (USW)	Standing waves form at the surface, but there is no broken water.
Fast riffle flow (FRF)	Very shallow, fast, flickering flow, still covering most of the substrata.
Rippled surface (RS)	The water surface has regular, smooth disturbances which form low transverse ripples across the direction of flow.
Slow riffle flow (SRF)	Very shallow, slower, flickering flow, still covering most of the substrata
Smooth boundary (and) turbulent (SBT)	The water surface remains smooth; medium to slow streaming flow takes place throughout the water profile; turbulence can be seen as the upward movement of fine suspended particles.
Trickle (TR)	Small, slow, shallow flow; when occurring with small or large cobbles, flow is between bed elements with few if any submerged.
Barely perceptible flow (BPF)	Smooth surface; flow only perceptible through the movement of floating objects or suspended matter.
No flow (NF)	No water movement.
Chaotic flow	Complex mixture of continuously varying flow types associated with unsteady, pulsating flow; common at high flows.
SUBSTRATUM CATEGORY (code)	SIZE RANGE (mm)
Silt (SI)	< 0.063
Sand (SA)	0.063 – 2
Small gravel (SG)	2 – 16
Large gravel (LG)	16 – 64
Small cobble (SC)	64 – 128
Large cobble (LC)	128 – 256
Boulder (B)	> 256
Bedrock (BR)	-

Appendix 3.5 **Summary of cross-section survey data collected for control and impact locations at each study site.** Corresponding trip survey dates are given in Appendix 3.1 and cross-section numbers in Figures 3.2-3.5 # WP - number of survey points in water, each identified by a patch code (Appendix 3.2); # DP - number of survey points on dry land, inclusive of water's edges; # WSEs - number of water surface elevations. Asterisks denote missing or inaccurate DWAF survey data excluded from analyses.

SITE	ELANDS						MOLENAARS						DU TOITS						RIVIERSONDEREND					
	Riffle			Run			Riffle			Run			Riffle			Run			Riffle			Run		
	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs	# WPs	# DPs	# WSEs
Control																								
Dec	19	40	5	18	20	4	13	34	4	16	27	5	16	8	3	17	14	3	12	23	4	14	18	4
Jan	23	45	5	20	25	5	15	35	5	16	33	5	17	9	5	17	17	5	17	25	5	17	20	5
Feb	30	54	5*	23	31	5*	20	35	5	20	28	5	17	19	5	13	29	5	15	34	5	17	29	5
Mar	30	48	5	25	24	5	23	33	5	20	26	5	17	13	5	15	24	5	19	25	5	16	21	5
Apr	29	39	5	24	21	5	25	36	5	20	27	5	14	12	5	18	26	5	32	14	5	22	13	5
May	27	35	3	20	17	3	26	27	4	17	26	3	16	8	3	20	21	3	17	9	3	18	9	3
Impact																								
Dec	22	28	5	15	15	4	18	37	6	16	30	5	13	9	3	13	7	3	15	21	4	15	25	5
Jan	24	23	5	17	16	5	21	47	5	25	37	5	14	6	5	13	9	5	17	23	5	19	24	5
Feb	23	42	5*	19	19	5*	24	53	5*	25	36	5*	11	23	5	17	24	5	16	35	5	14	38	5
Mar	25	33	5	18	20	5	27	47	5	26	29	5	14	24	5*	15	29	5*	17	22	5	27	23	5
Apr	28	27	5	16	15	5	34	29	5	26	23	4	19	16	5*	33	13	5*	25	15	5	31	17	5
May	26	16	3	20	10	3	30	27	3	27	22	3	18	5	3	20	8	3	20	16	3	27	16	3

Appendix 3.6 Modified Wentworth grade scale for substratum classification (adapted from King and Tharme 1994).

SUBSTRATUM	TYPE	GRADE LIMITS (mm)	PHI RANGE FOR GRADE (Φ)	DESCRIPTION AND BROAD CATEGORY USED IN PRESENT STUDY		GRADE LIMITS (mm)
BEDROCK	Bedrock	Not specified	Not specified	Bedrock	Particle size classes grouped as ***bedrock***	X > 2048
	Very large boulder	2048 < X ≤ 4096	-11 < X ≤ -12	Very large boulder		
	Large boulder	1024 < X ≤ 2048	-10 < X ≤ -11	Large boulder	Particle size classes grouped as ***boulder***	256 < X ≤ 2048
	Medium boulder	512 < X ≤ 1024	-9 < X ≤ -10	Medium boulder		
	Small boulder	256 < X ≤ 512	-8 < X ≤ -9	Small boulder		
	Large cobble	128 < X ≤ 256	-7 < X ≤ -8	Large cobble	Particle size classes grouped as ***cobble***	64 < X ≤ 256
GRAVEL	Small cobble	64 < X ≤ 128	-6 < X ≤ -7	Small cobble		
	Very coarse pebble	32 < X ≤ 64	-5 < X ≤ -6	Large gravel	Particle size classes grouped as ***gravel***	2 < X ≤ 64
	Coarse pebble	16 < X ≤ 32	- 4 < X ≤ -5	Medium gravel		
	Medium pebble	8 < X ≤ 16	-3 < X ≤ -4	Medium gravel		
	Fine pebble	4 < X ≤ 8	-2 < X ≤ -3	Small gravel		
	Very fine pebble	2 < X ≤ 4	-1 < X ≤ -2	Small gravel		
	Very coarse sand	1 < X ≤ 2	0 < X ≤ -1	Very coarse sand	Particle size classes grouped as ***sand***	1/16 < X ≤ 2
	Coarse sand	1/2 < X ≤ 1	+1 < X ≤ 0	Coarse sand		
SAND	Medium sand	1/4 < X ≤ 1/2	+2 < X ≤ +1	Medium sand		
	Fine sand	1/8 < X ≤ 1/4	+3 < X ≤ +2	Fine sand		
	Very fine sand	1/16 < X ≤ 1/8	+4 < X ≤ +3	Very fine sand		
	Coarse silt	1/32 < X ≤ 1/16	+5 < X ≤ +4	silt	Particle size classes grouped as ***silt*** (with any organic detritus)	1/256 < X ≤ 1/16
	Medium silt	1/64 < X ≤ 1/32	+6 < X ≤ +5	silt		
	Fine silt	1/128 < X ≤ 1/64	+7 < X ≤ +6	silt		
	Very fine silt	1/256 < X ≤ 1/128	+8 < X ≤ +7	silt		
MUD	Coarse clay	1/512 < X ≤ 1/256	+9 < X ≤ +8	clay	Particle size classes grouped as ***clay***	X ≤ 1/256
	Medium clay	1/1024 < X ≤ 1/512	+10 < X ≤ +9	clay		
	Fine clay	1/2048 < X ≤ 1/1024	+11 < X ≤ +10	clay		
	Very fine clay	1/4096 < X ≤ 1/2048	+12 < X ≤ +11	clay		

Appendix 3.7 Determination of relationships between river stone size and surface area, for calculating sample invertebrate abundances per 0.1 m^2.

Introduction

Numerous methods have been used to estimate the surface area of individual river stones for benthic ecological studies (Calow 1972; Minshall and Minshall 1977; Dall 1979; Doeg and Lake 1981; Godbout and Hynes 1982; McAuliffe 1984; Hooper and Ottey 1988; Graham *et al.* 1988; Biggs and Close 1989; Death and Winterbourn 1995; Scarsbrook and Townsend 1993; Matthaei *et al*. 2000; Ledger and Hildrew 2001; Riseng *et al.* 2004). These range from commonly adopted, simple empirical determinations of surface areas by wrapping individual stones (e.g. in aluminium foil, plastic, acetate, latex, of known mass per unit area) or from image analysis (Riseng *et al.* 2004)., to various empirical or theoretical formulae (e.g. equations for spherical and ellipsoid approximations of surface area) based on surface area-axis relationships for one or more easily measured axes or perimeters (Figure 3.9 illustrates the three primary stone axes: α (L), β (W) and c (H)). For example, stone length x width was used as a simple estimate of the area of upper stone surfaces by McAuliffe (1984) in an experimental study. Surface areas of individual river stones from which invertebrates were sampled were measured using a plastic grid by Hooper and Ottey (1988). Graham *et al.* (1988) examined several approaches recommended in the literature, including the use of a modified formula for sphere surface area ($4\pi r^2$) by Dall (1979):

$$\text{Surface area} = 4\pi \{(LxW) + (WxH) + (HxL)/12\} \qquad \textbf{Equation A3.7.1}$$

Graham *et al.* (1988) found that the surface area of stones can be precisely estimated from linear regression equations of area on a two-dimensional term of the form (xy + yz + zx) where x, y and z are either the axial dimensions or the axial perimeters of stones; the combined axes term was adapted from Dall's (1979) spherical approximation approach. They developed the following linear regression equation for New Zealand smooth, well-worn river stones from the Waitaki River, based on a sample of n = 14 stones, ranging from 90-200 mm in length:

$$\text{Whole stone surface area} = 1.15 \times \{(LxW) + (WxH) + (HxL)\} \qquad \textbf{Equation A3.7.2}$$

The mean percentage error of estimation and SD of the method, using axes (not perimeters), were 3.9%, and 3.1%, respectively. These values were found to be considerably less than errors of estimation for other methods applied to the same sample of stones. Regression lines determined by a least squares method produced the same slope, to two decimal places, as the method of minimizing mean percentage absolute error. Graham *et al.* (1988) indicated that the specific slopes of the regression lines of the equation for surface area might differ for stones from different environments. The same approach based on composite stone dimensions was employed by Biggs and Close (1989), with a regression line applicable to nine different river sites derived from 107 greywacke rocks (approx. 20 from each of five of the sites).

Methods

For this study, the following steps were undertaken:

(1) Development of a unique regression equation for the river stones sampled at the four study sites, based on the general form of the equation (i.e. same combined axes term) recommended by Graham *et al.* (1988).
(2) Development of independent regression equations for each stone axis.
(3) Comparison of the first two approaches with multiple regression analysis using the three axes in addition to the combined axes term.
(4) Comparison of approaches (1)-(3) with surface area estimates obtained using a mathematical algorithm based on an approximation of ellipsoid surface area (Maple V program, ellipsoidal algorithm) and with Graham *et al.*'s (*op. cit.*) regression equation specific for New Zealand river stones.

A total of 20 stones was selected from across all eight locations at the four sites, to represent commonly sampled stone sizes. They ranged from β_{min} = 70 mm (small cobble) to β_{max} = 148 mm (large cobble) and spanned the range of shapes encountered, from angular to well-rounded. Each of the stones was foil wrapped and the individual surface areas estimated from an area versus foil weight relationship, developed using four control foil squares (100 x 100 mm, consistent in mass (g) to two decimal places). These measured surface areas were used as the dependent variable in the regression analyses. The three axes of the stones were measured using a flexible measuring tape, as done in the field for every stone from which invertebrates were sampled (Sections 3.4 and 3.5). The combined axes term was then calculated as per Equation A3.7.2. Simple linear and multiple regression analyses were performed using the Visual General Linear Model module of STATISTICA 6.1. Two-tailed tests of the significance of the regressions were performed using a Student's *t* test for the linear regression and ANOVA for the multiple regression.

Results and discussion

The results of simple linear regression of stone surface area on stone axial dimensions are given in Table A3.7.1.

Table A3.7.1 Results of simple linear regression analysis of stone surface area on stone axial dimensions. SE - Standard Error. Cnf. Lmt. - Confidence limit.

EFFECT	SURFACE AREA PARAMETER	*t* statistic	*P*	β	SE β	-95% Cnf. Lmt.	+95% Cnf. Lmt.
α (L) axis	377.646	20.531	< 0.001	0.978	0.048	0.878	1.078
β (W) axis	506.496	21.315	< 0.001	0.980	0.046	0.884	1.076
c (H) axis	920.420	21.789	< 0.001	0.981	0.045	0.886	1.075
Combined axes term {(LxW) + (WxH) + (HxL)}	1.899	38.812	< 0.001	0.994	0.026	0.940	1.047

Although all regression relationships were highly significant ($P < 0.001$), the best fit relationship was obtained for the combined axes term ($R^2 = 0.99$; Figure A3.7.1). Multiple regression analysis using all three axes individually plus the combined axes term, produced a significant relationship overall ($F_{4, 16} = 495.92$, adjusted $R^2 = 0.99$, $P < 0.001$), but only the partial regression coefficient for the combined term was significant. Comparison of regression results with surface area estimates obtained using the ellipsoid approximation and Equation A3.7.2 supported the adoption of a modified, study-specific form of the latter equation as most appropriate.

The form of the equation used in this study, therefore, to calculate surface areas for sample stones for comparisons across samples (per 0.1 m^2 unit surface area) is:

$$y = 1.899 \times \{(LxW) + (WxH) + (HxL)\} \qquad \textbf{Equation A3.7.3}$$

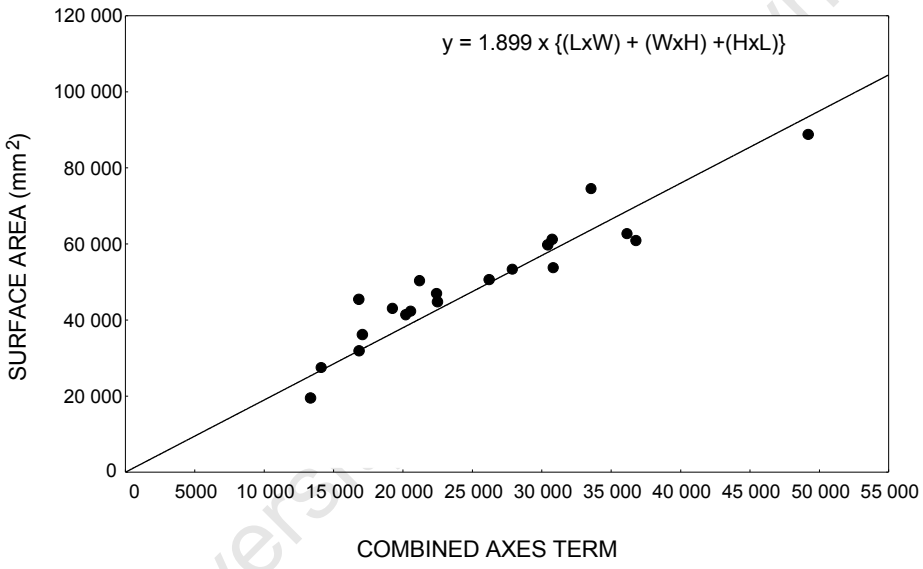


Figure A3.7.1 Scatterplot of the combined axes term {(LxW) + (WxH) + (HxL)} against stone surface area measured empirically by foil wrapping (*n* = 20). The linear regression relationship is superimposed (y-intercept = 0).

Appendix 4.1 Natural average daily discharges (m^3 s^{-1}) corresponding with a standard range of percentage exceedence values (Q_1-Q_{99}) derived from daily flow duration curves (FDCs) for the sites. Flow percentiles were calculated from annual, month-specific (for the six months corresponding with the study) and peak dry season ('Dry', Jan-Mar) FDCs generated from natural historical flow records for each site. Additional percentiles (Q_{25} and Q_{75}) were calculated for FDCs for individual months. Percentiles are approximate, in particular the Q_1 and Q_{99} values which define upper and lower flow extremes, respectively.

PERCENTILE (Q_n)	1	5	10	20	25	30	40	50	60	70	75	80	90	95	99
MOLENAARS															
Annual FDC	51.410	19.410	9.950	5.070	-	3.270	2.310	1.640	1.190	0.820	-	0.610	0.480	0.440	0.330
Monthly FDC															
Dec	17.450	4.168	2.500	1.580	1.348	1.200	0.990	0.890	0.800	0.730	0.706	0.670	0.600	0.561	0.520
Jan	4.660	2.221	1.550	0.940	0.805	0.730	0.670	0.623	0.590	0.550	0.527	0.510	0.470	0.438	0.380
Feb	3.320	1.638	1.180	0.740	0.685	0.610	0.560	0.517	0.480	0.460	0.442	0.440	0.390	0.338	0.210
Mar	14.620	2.246	1.400	0.860	0.698	0.650	0.580	0.517	0.490	0.470	0.458	0.440	0.400	0.368	0.310
Apr	22.820	8.664	4.220	2.060	1.660	1.410	1.080	0.757	0.580	0.510	0.490	0.460	0.400	0.358	0.280
May	63.790	30.770	16.620	6.780	4.542	3.810	2.580	1.710	1.320	1.000	0.889	0.730	0.520	0.452	0.370
Dry FDC	7.050	1.910	1.380	0.860	-	0.680	0.610	0.560	0.520	0.490	-	0.460	0.420	0.380	0.280
ELANDS															
Annual FDC	35.510	12.190	5.920	2.700	-	1.770	1.270	0.930	0.650	0.490	-	0.380	0.280	0.250	0.200
Monthly FDC															
Dec	8.790	1.910	1.260	0.850	0.763	0.680	0.580	0.521	0.470	0.430	0.414	0.390	0.350	0.317	0.280
Jan	2.670	1.211	0.890	0.580	0.507	0.480	0.420	0.374	0.350	0.310	0.301	0.290	0.270	0.251	0.230
Feb	1.990	0.755	0.640	0.510	0.431	0.430	0.370	0.316	0.290	0.270	0.257	0.250	0.230	0.209	0.150
Mar	14.990	1.116	0.800	0.480	0.452	0.430	0.390	0.327	0.290	0.260	0.255	0.250	0.230	0.209	0.160
Apr	17.480	10.420	3.630	1.380	1.100	0.880	0.620	0.461	0.380	0.300	0.284	0.270	0.230	0.209	0.180
May	37.340	17.760	12.240	4.530	2.964	2.360	1.650	1.018	0.810	0.620	0.538	0.520	0.410	0.263	0.220
Dry FDC	4.870	1.100	0.750	0.520	-	0.440	0.400	0.350	0.310	0.280	-	0.260	0.240	0.220	0.160

Appendix 4.1 Continued.

PERCENTILE (Q_n)	1	5	10	20	25	30	40	50	60	70	75	80	90	95	99
DU TOITS															
Annual FDC	5.990	3.930	2.590	1.530	-	0.970	0.660	0.440	0.320	0.240	-	0.190	0.160	0.140	0.120
Monthly FDC															
Dec	2.990	2.280	0.670	0.410	0.364	0.330	0.300	0.266	0.240	0.220	0.215	0.210	0.190	0.170	0.150
Jan	2.450	0.468	0.400	0.290	0.252	0.230	0.200	0.190	0.180	0.170	0.167	0.160	0.150	0.129	0.090
Feb	0.930	0.428	0.350	0.250	0.206	0.190	0.180	0.171	0.160	0.160	0.154	0.150	0.140	0.127	0.120
Mar	3.660	0.866	0.410	0.240	0.219	0.200	0.180	0.167	0.150	0.150	0.145	0.140	0.130	0.127	0.120
Apr	4.460	1.820	1.150	0.550	0.428	0.370	0.280	0.214	0.180	0.160	0.148	0.140	0.120	0.120	0.100
May	6.050	4.690	3.470	1.750	1.410	1.100	0.780	0.556	0.410	0.310	0.275	0.240	0.190	0.151	0.120
Dry FDC	2.430	0.670	0.380	0.260	-	0.210	0.190	0.180	0.170	0.160	-	0.150	0.140	0.130	0.120
RIVIERSONDEREND															
Annual FDC	19.400	9.300	4.950	2.120	-	1.200	0.800	0.560	0.400	0.280	-	0.200	0.150	0.130	0.100
Monthly FDC															
Dec	9.700	2.130	1.100	0.570	0.409	0.420	0.320	0.251	0.230	0.200	0.182	0.180	0.150	0.135	0.070
Jan	4.360	1.210	0.650	0.360	0.274	0.260	0.210	0.172	0.160	0.150	0.139	0.139	0.120	0.110	0.100
Feb	3.830	0.937	0.550	0.300	0.267	0.240	0.200	0.174	0.150	0.140	0.129	0.120	0.110	0.097	0.080
Mar	8.180	2.580	1.030	0.440	0.355	0.300	0.240	0.195	0.180	0.160	0.148	0.140	0.130	0.106	0.090
Apr	13.900	6.630	3.890	1.520	1.090	0.860	0.550	0.419	0.300	0.200	0.182	0.160	0.130	0.116	0.090
May	23.700	14.700	8.410	3.650	2.540	1.970	1.240	0.836	0.590	0.440	0.371	0.340	0.240	0.165	0.120
Dry FDC	6.060	1.490	0.710	0.370	-	0.260	0.220	0.180	0.160	0.150	-	0.130	0.120	0.110	0.090

Appendix 4.2 (a) State matrices for determining Colwell's indices based on the standard seven default flow classes ranging from <0.5 $\overline{Q}$ ->3 $\overline{Q}$ (Section 3.2.3) for the four study sites. $\overline{Q}$ is represented by monthly flow volumes (Mcm) calculated for water years, and is highlighted by shading. Results derived from flows expressed as average monthly discharges ($m^3 s^{-1}$) yielded the same results.

SITE	FLOW CLASS (Mcm)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
MOLENAARS	< 6.096	25	27	25	18	8	2	1	0	1	11	22	22
	to 12.192	2	0	1	7	1	3	2	1	8	8	2	3
	to 18.288	0	0	1	1	8	6	3	8	11	5	2	2
	to 24.384	0	0	0	1	4	3	3	6	2	3	1	0
	to 30.480	0	0	0	0	4	2	6	7	3	0	0	0
	to 36.576	0	0	0	0	0	4	6	3	1	0	0	0
	> 36.576	0	0	0	0	2	7	6	2	1	0	0	0
ELANDS	< 4.086	25	27	24	18	5	2	1	0	6	13	24	24
	to 8.172	2	0	2	6	4	4	5	5	6	10	0	1
	to 12.258	0	0	0	2	10	6	4	7	9	3	2	2
	to 16.344	0	0	1	0	3	7	6	11	3	1	1	0
	to 20.430	0	0	0	0	2	1	4	1	2	0	0	0
	to 24.515	0	0	0	0	1	2	3	2	1	0	0	0
	> 24.515	0	0	0	1	2	5	4	1	0	0	0	0
DU TOITS	< 1.562	25	27	23	18	6	3	1	0	0	9	21	22
	to 3.123	0	0	3	8	5	3	2	1	11	11	3	2
	to 4.685	2	0	0	1	8	4	6	5	4	3	2	2
	to 6.246	0	0	1	0	3	5	0	6	4	3	0	0
	to 7.808	0	0	0	0	2	5	6	7	7	1	1	1
	to 9.370	0	0	0	0	2	2	8	5	1	0	0	0
	> 9.370	0	0	0	0	1	5	4	3	0	0	0	0
RIVIERSONDEREND	< 2.558	25	27	22	11	3	2	0	0	0	8	20	19
	to 5.115	1	0	2	8	6	2	2	1	7	11	5	6
	to 7.673	1	0	3	7	6	5	7	6	12	6	1	2
	to 10.231	0	0	0	1	5	5	2	7	4	1	1	0
	to 12.789	0	0	0	0	2	6	7	8	3	1	0	0
	to 15.346	0	0	0	0	4	4	7	2	1	0	0	0
	> 15.346	0	0	0	0	1	3	2	3	0	0	0	0

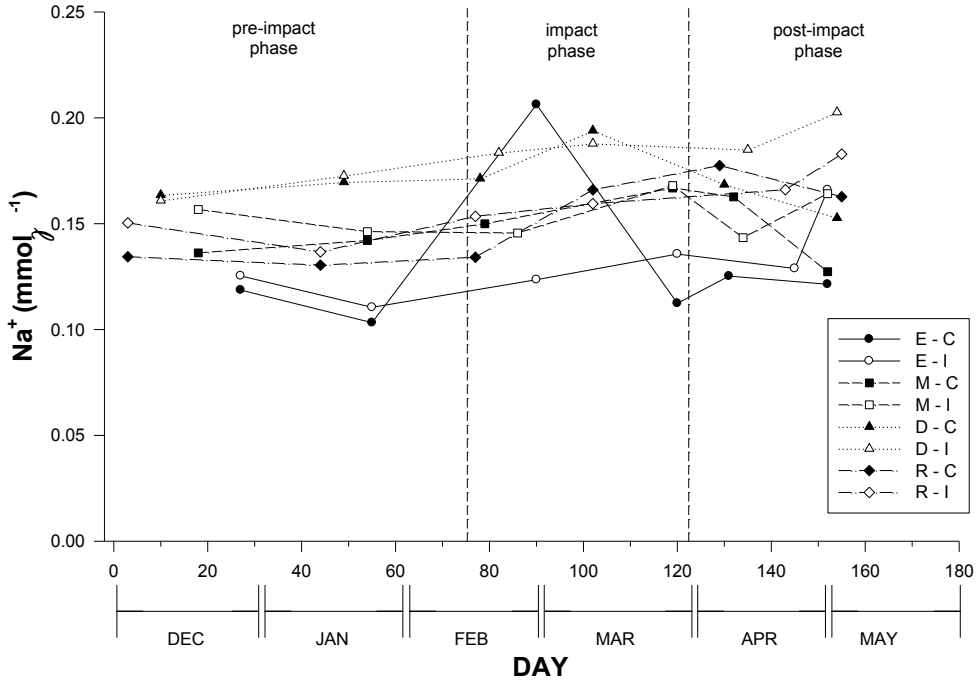
Appendix 4.2 (b) State matrices for determining Colwell's indices based on 15 flow classes focused on the low flow component of the hydrological regime, ranging from <0.125 $\overline{Q}$ ->1.750 $\overline{Q}$ (Section 3.2.3). $\overline{Q}$ is represented by monthly flow volumes (Mcm) calculated for water years, and is highlighted by shading. Results derived from flows expressed as average monthly discharges ($m^3 s^{-1}$) yielded the same results.

SITE	FLOW CLASS (Mcm)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
MOLENAARS	< 1.524	5	16	9	6	0	0	0	0	0	0	0	0
	to 3.048	18	9	13	7	2	1	1	0	0	1	10	14
	to 4.572	1	2	2	2	4	1	0	0	0	4	8	6
	to 6.096	1	0	1	3	2	0	0	0	1	6	4	2
	to 7.620	0	0	0	1	0	1	0	0	5	3	2	2
	to 9.144	2	0	0	4	0	1	1	1	2	4	0	0
	to 10.668	0	0	1	1	1	0	0	0	1	1	0	0
	to 12.192	0	0	0	1	0	1	1	0	0	0	0	1
	to 13.716	0	0	0	0	0	1	2	1	3	2	0	0
	to 15.240	0	0	0	0	3	1	1	3	1	1	0	0
	to 16.764	0	0	1	0	1	1	0	2	3	1	2	1
	to 18.288	0	0	0	1	4	3	0	2	4	1	0	1
	to 19.812	0	0	0	0	3	1	0	1	0	0	0	0
	to 21.336	0	0	0	1	0	1	1	3	2	0	1	0
	> 21.336	0	0	0	0	7	14	20	14	5	3	0	0
ELANDS	< 1.021	11	18	13	6	0	0	0	0	0	0	1	2
	to 2.043	13	7	9	8	3	2	1	0	0	2	12	16
	to 3.064	1	2	1	2	2	0	0	0	0	6	8	2
	to 4.086	0	0	1	2	0	0	0	0	6	5	3	4
	to 5.108	1	0	1	4	2	2	1	0	1	5	0	0
	to 6.129	1	0	0	1	1	1	0	1	1	1	0	1
	to 7.150	0	0	0	0	0	1	3	1	2	2	0	0
	to 8.172	0	0	1	1	1	0	1	3	2	2	0	0
	to 9.193	0	0	0	0	4	2	0	2	6	0	2	1
	to 10.215	0	0	0	0	4	2	0	2	2	0	0	1
	to 11.236	0	0	0	1	1	2	1	3	1	0	0	0
	to 12.258	0	0	0	1	1	0	3	0	0	3	0	0
	to 13.280	0	0	1	0	0	2	1	6	1	1	1	0
	to 14.301	0	0	0	0	0	0	2	2	0	0	0	0
	> 14.301	0	0	0	1	8	13	14	7	5	0	0	0

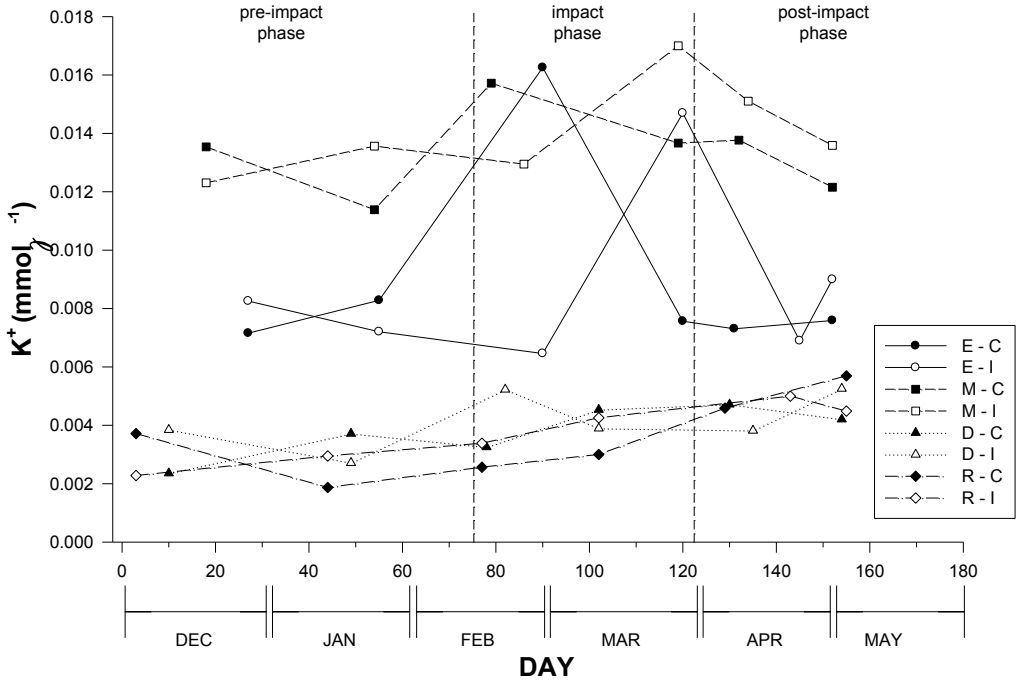
Appendix 4.2 (b) Continued.

SITE	FLOW CLASS (Mcm)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
DU TOITS	< 0.390	2	6	5	4	0	0	0	0	0	0	0	0
	to 0.780	20	15	15	5	2	1	0	0	0	0	4	15
	to 1.171	1	5	3	6	2	1	1	0	0	3	13	4
	to 1.561	2	1	0	3	2	1	0	0	0	6	4	3
	to 1.952	0	0	1	2	1	0	1	0	3	2	1	2
	to 2.342	0	0	2	0	0	2	0	0	1	1	2	0
	to 2.732	0	0	0	3	2	1	1	0	4	5	0	0
	to 3.123	0	0	0	3	2	0	0	1	3	3	0	0
	to 3.513	0	0	0	0	2	0	1	1	2	0	1	2
	to 3.903	1	0	0	0	2	1	1	2	0	2	0	0
	to 4.294	0	0	0	1	3	2	2	2	2	1	1	0
	to 4.684	1	0	0	0	1	1	2	0	0	0	0	0
	to 5.075	0	0	1	0	1	1	0	1	2	1	0	0
	to 5.465	0	0	0	0	0	3	0	3	0	0	0	0
	> 5.465	0	0	0	0	7	13	18	17	10	3	1	1
RIVIERSONDEREND	< 0.639	10	14	7	2	0	0	0	0	0	0	0	7
	to 1.278	10	8	10	5	0	0	0	0	0	4	8	8
	to 1.918	4	2	4	2	1	2	0	0	0	2	7	4
	to 2.557	1	3	1	2	2	0	0	0	0	2	5	0
	to 3.197	1	0	1	3	1	0	1	0	2	3	3	4
	to 3.836	0	0	0	1	1	0	0	0	3	3	2	1
	to 4.475	0	0	0	2	2	0	1	0	0	0	0	1
	to 5.115	0	0	1	2	2	2	0	1	2	5	0	0
	to 5.754	1	0	2	3	0	2	2	1	1	0	0	0
	to 6.393	0	0	1	3	1	1	2	2	6	3	0	1
	to 7.033	0	0	0	1	1	0	2	0	3	1	1	0
	to 7.672	0	0	0	0	4	2	1	3	2	2	0	1
	to 8.312	0	0	0	0	0	2	0	2	2	0	0	0
	to 8.951	0	0	0	0	2	1	0	4	0	0	1	0
	> 8.951	0	0	0	1	10	15	18	14	6	2	0	0

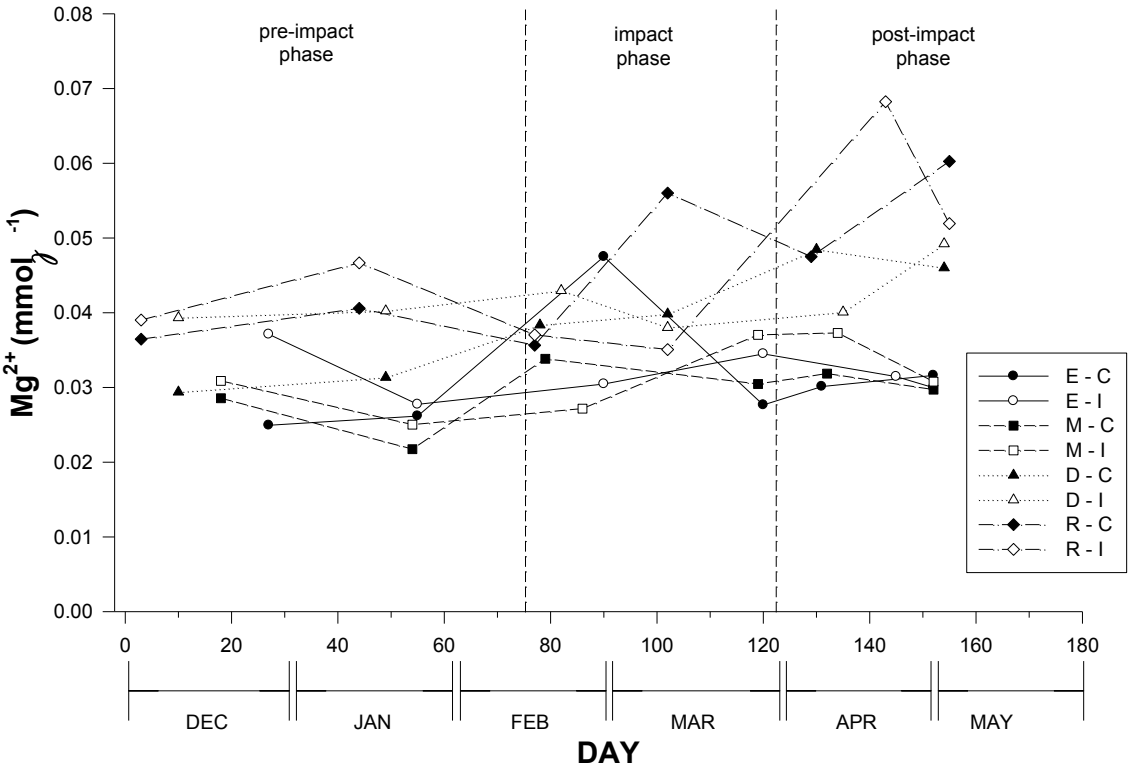
Appendix 5.1 Changes in water chemistry at the sites during the different phases of the low flow study. Demarcation of the impact phase is approximate. Sites: Elands (E); Molenaars (M); Du Toits (D); and Riviersonderend (R). Locations: C - control; I - impact. Trends in conductivity, dissolved oxygen and pH are illustrated in the text.



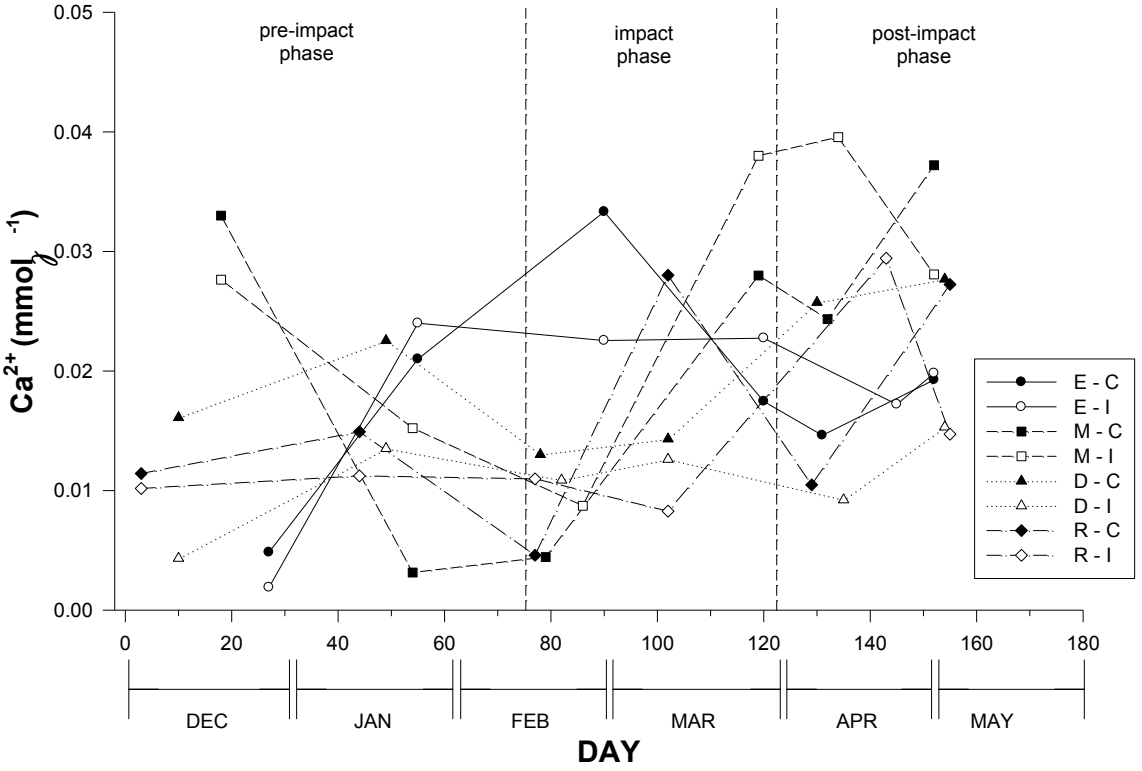
(a) Na^+ (mmol ℓ^{-1}).



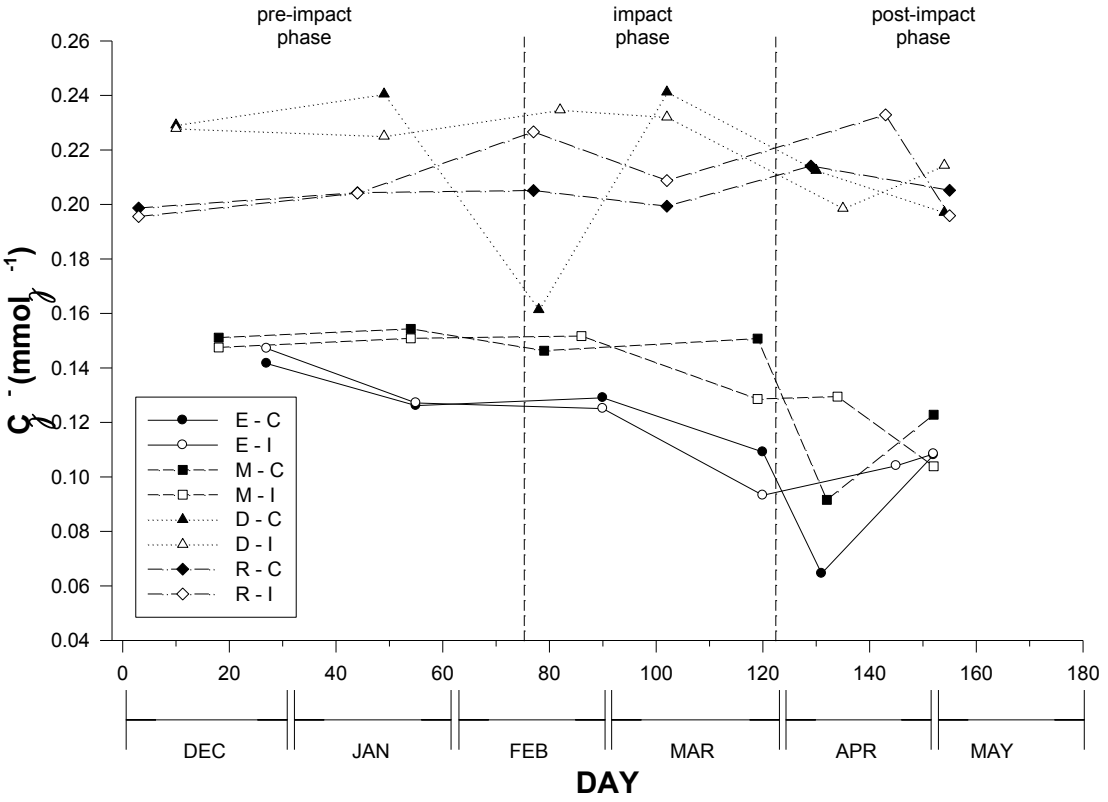
(b) K^+ (mmol ℓ^{-1}).



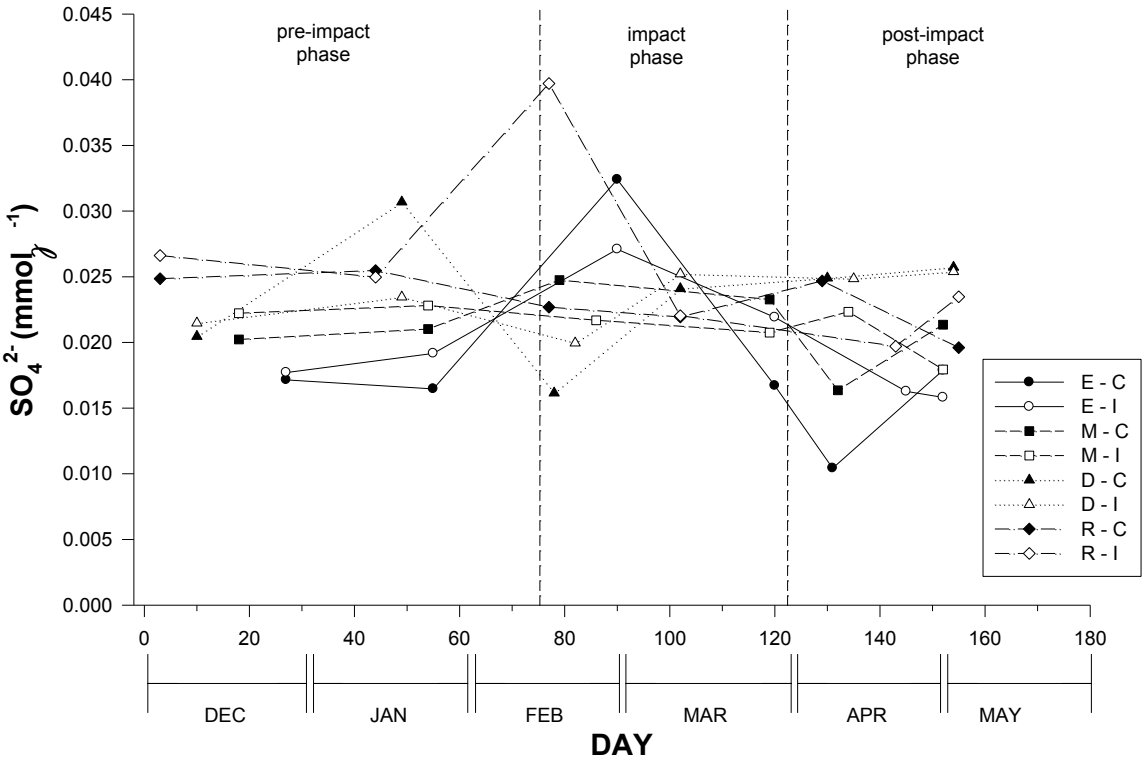
(c) Mg^{2+} (mmol ℓ^{-1}).



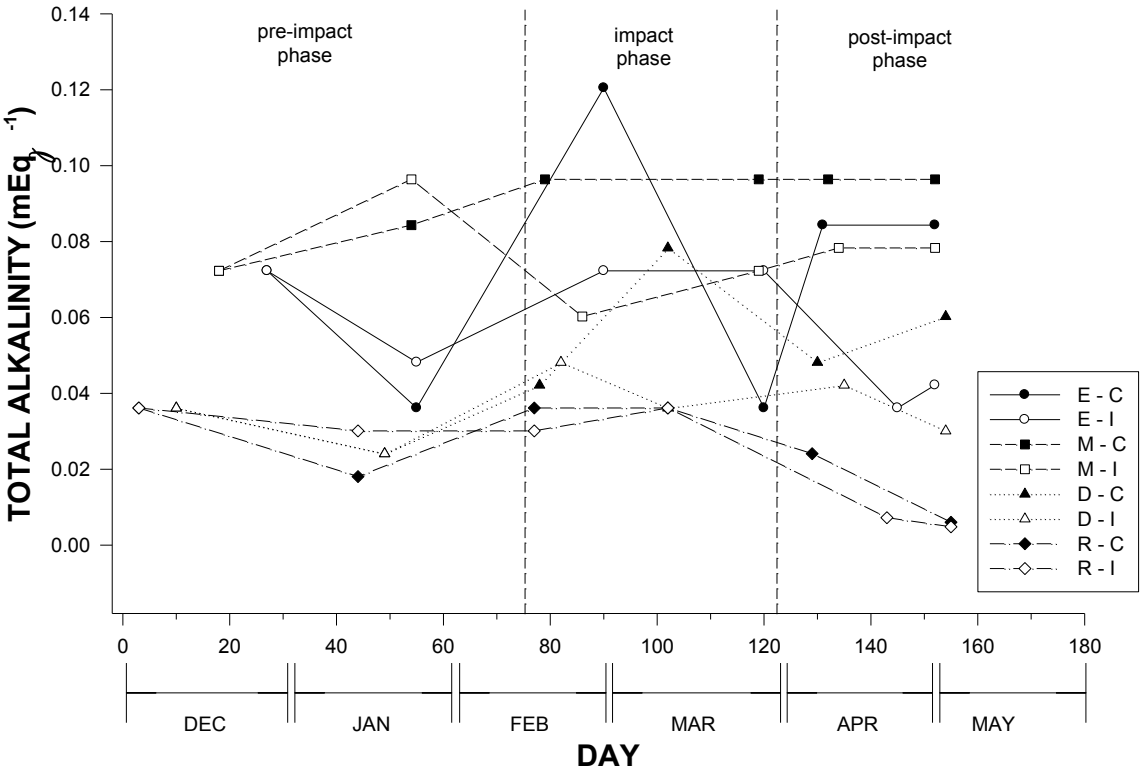
(d) Ca^{2+} (mmol ℓ^{-1}).



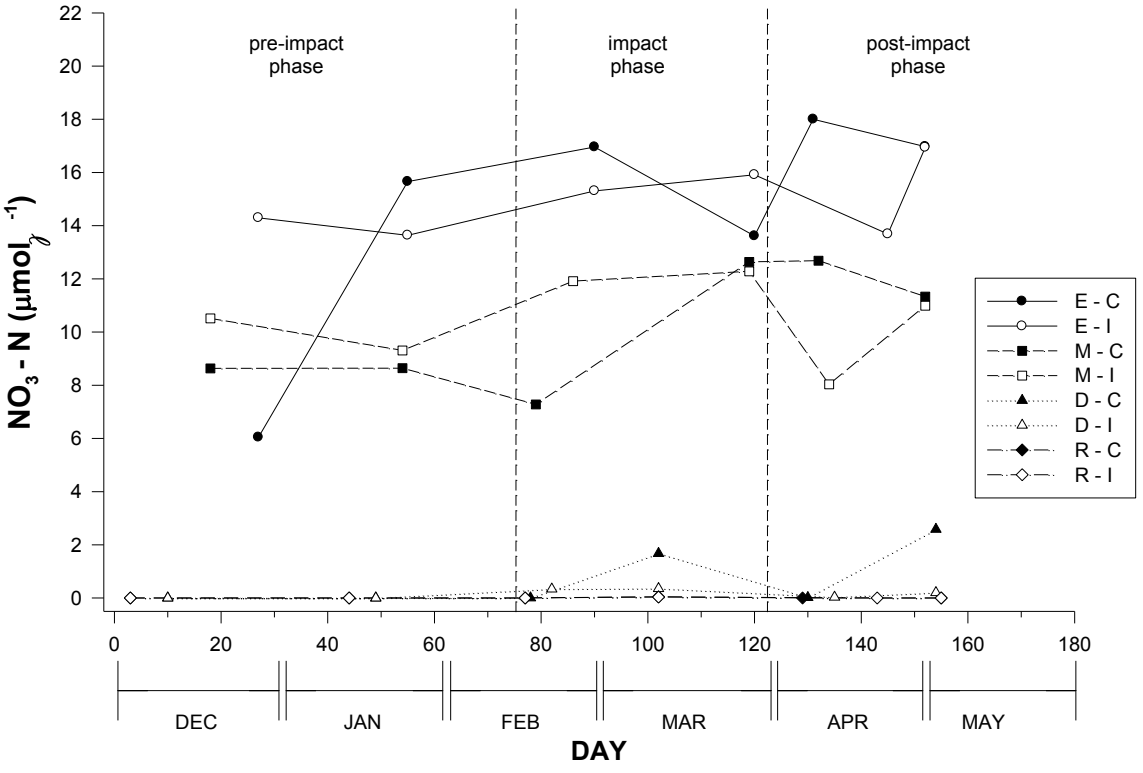
(e) Cℓ^- (mmol ℓ^{-1}).



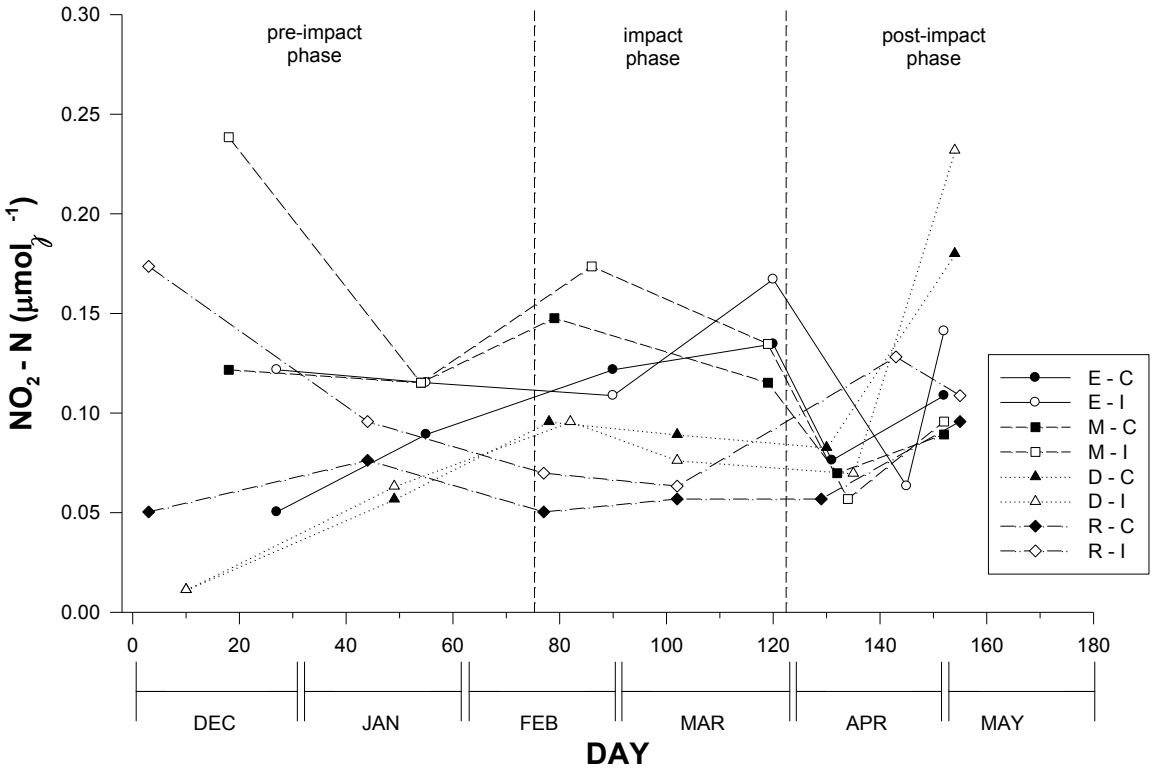
(f) SO_4^{2-} (mmol ℓ^{-1}).



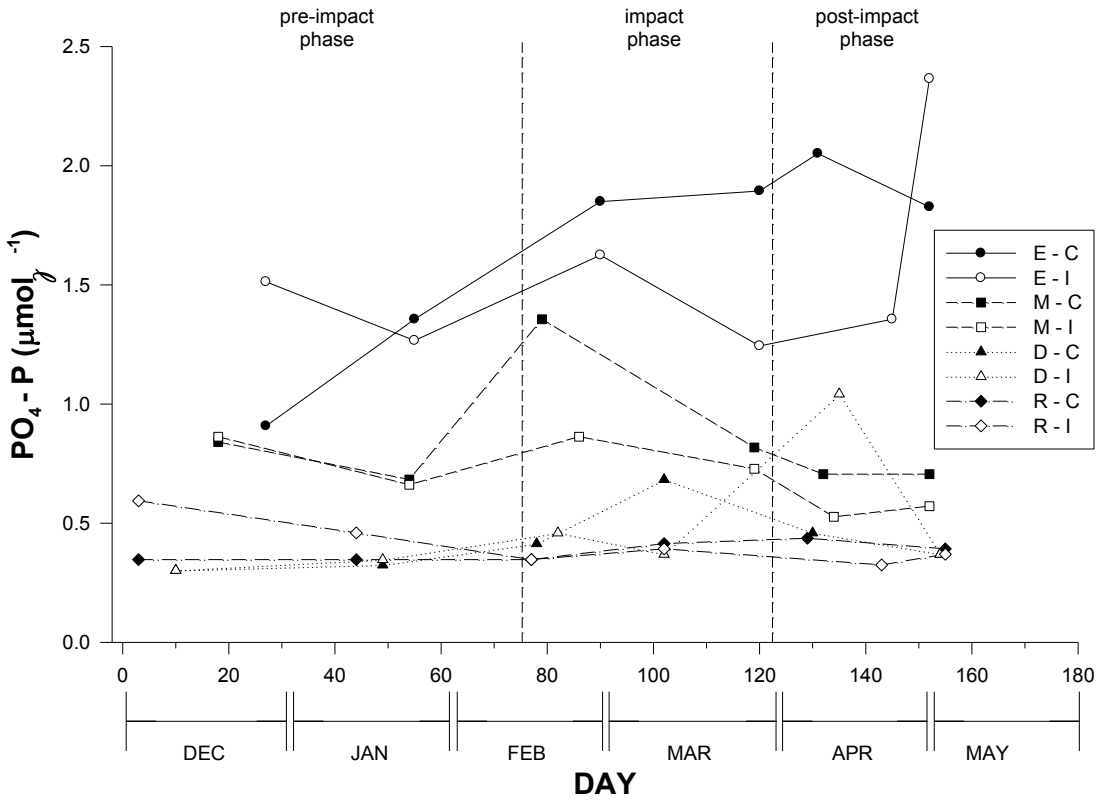
(g) Total alkalinity (mEq ℓ^{-1}).



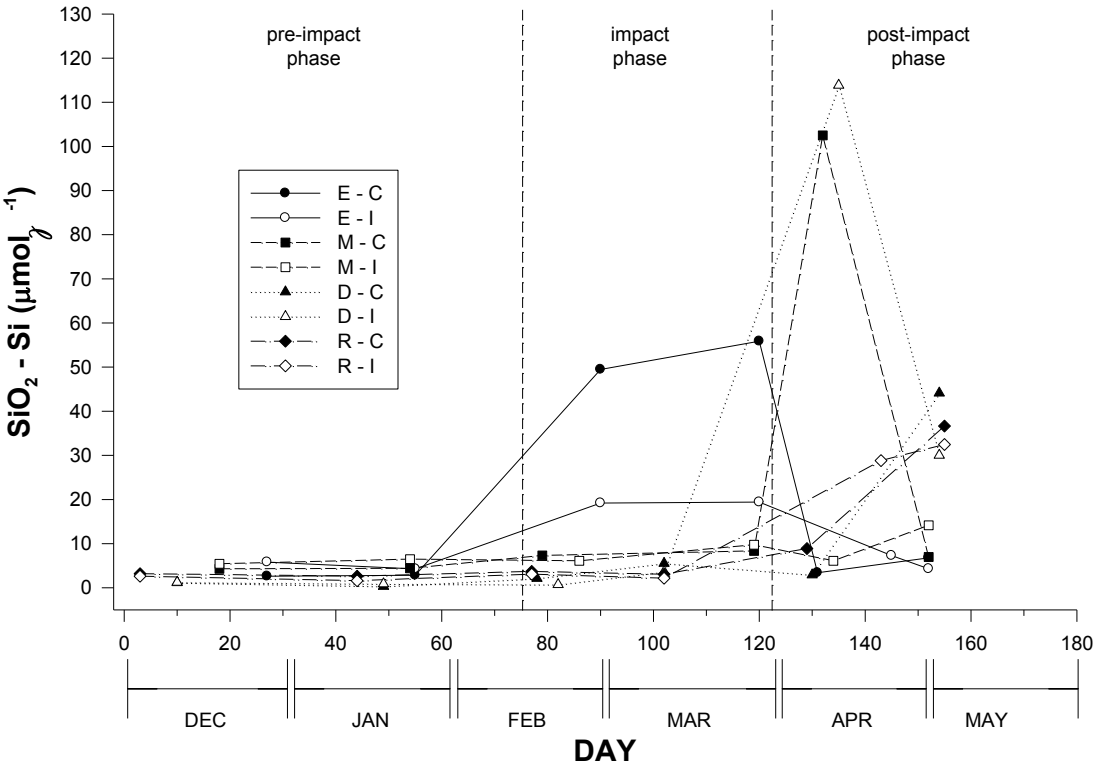
(h) Nitrate (μmol ℓ^{-1}).



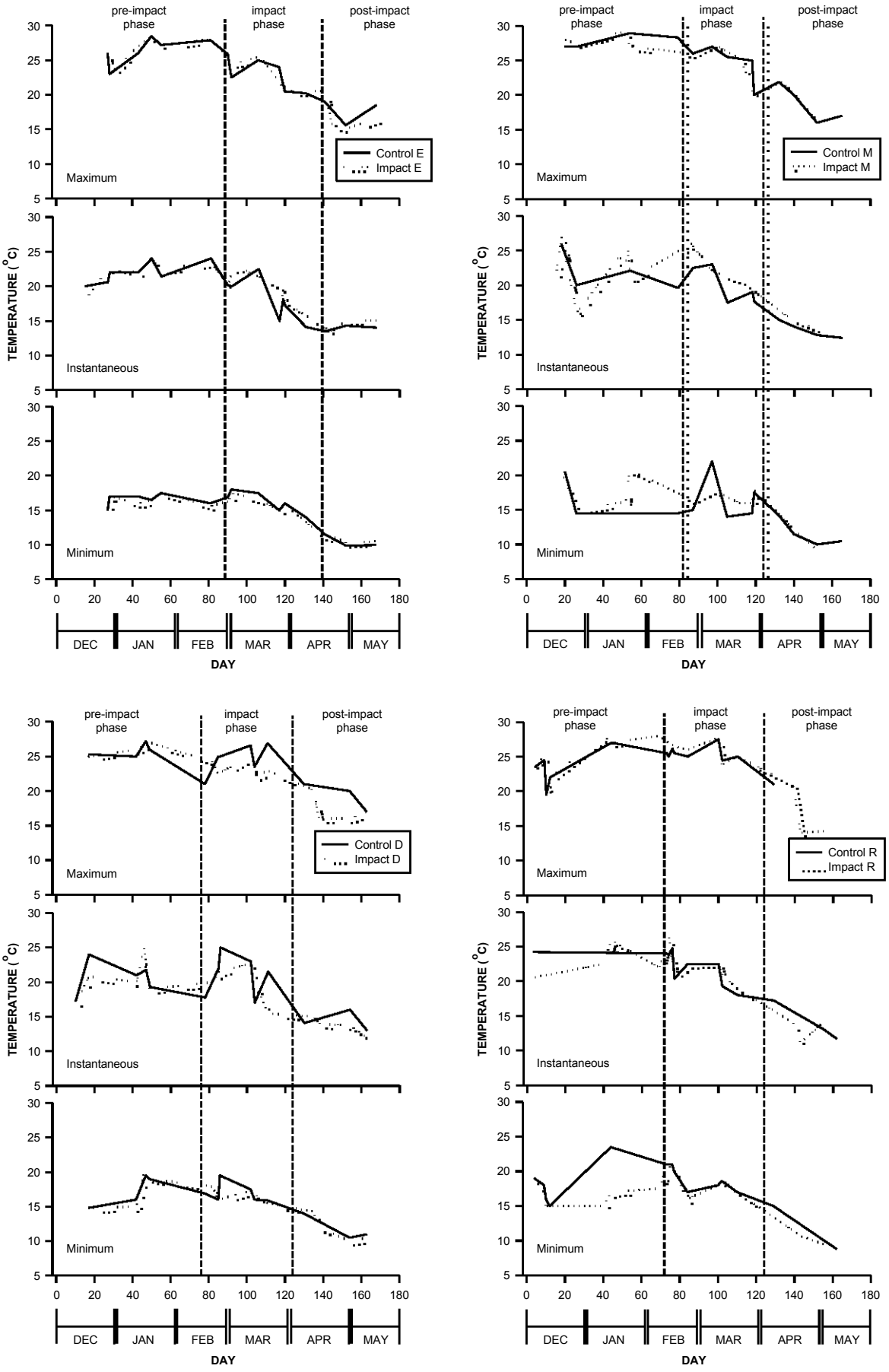
(i) Nitrite (μmol ℓ^{-1}).



(j) Phosphate (μmol ℓ^{-1}).

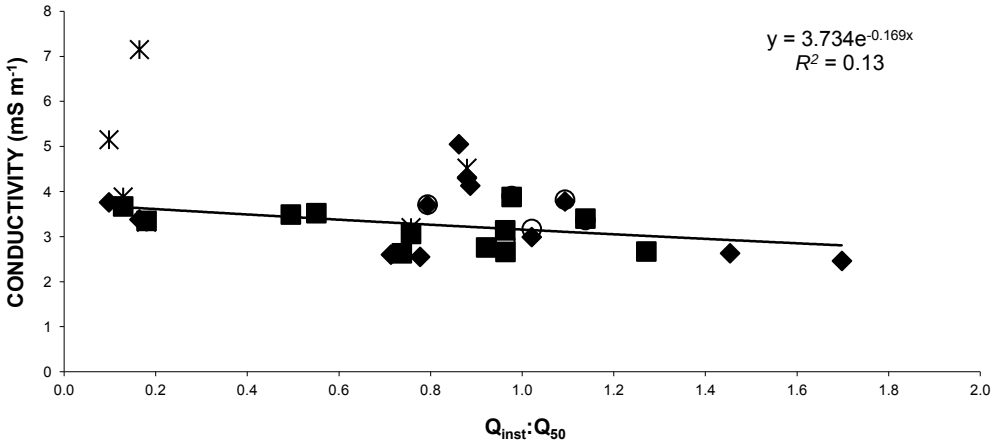


(k) Silicon (µmol ℓ^{-1}).

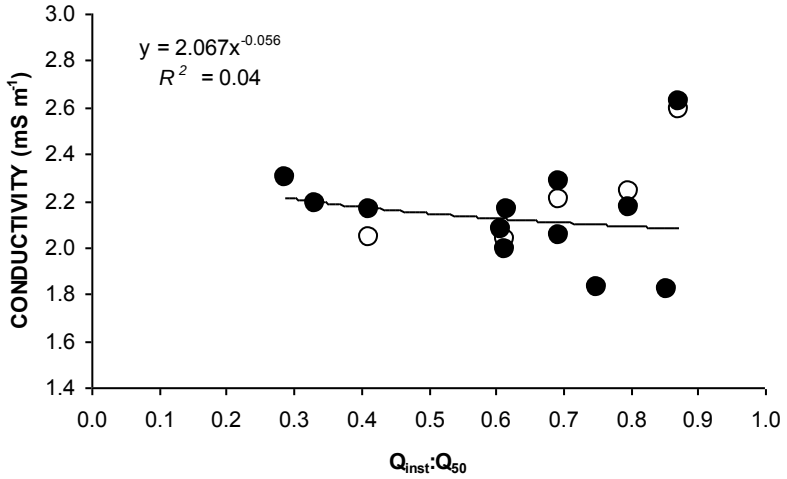


(I) Temperature (°C).

Appendix 5.2 Concentration-discharge relationships for select water chemistry variables at low flows.

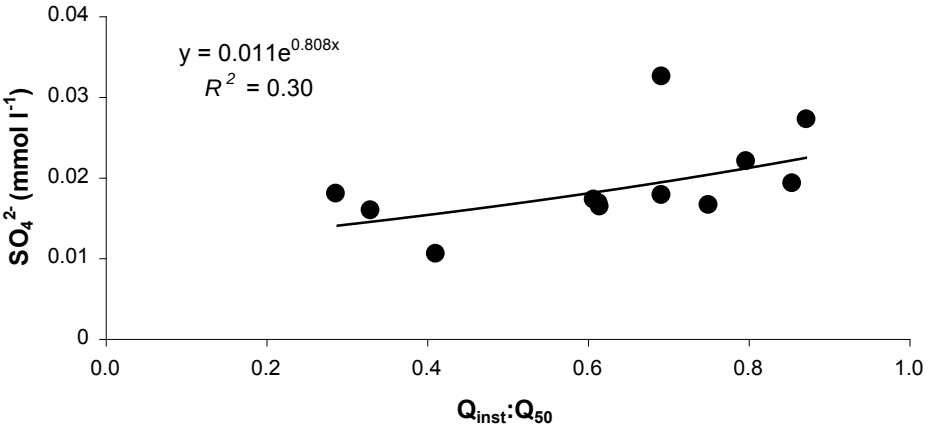


(a) **Changes in mainstream conductivity with discharge for combined data from the Du Toits (solid squares) and Riviersonderend (solid diamonds) sites.** The best-fit trend line is shown. Open circles and stars indicate values for isolated pools under natural and unnatural low flows, respectively.

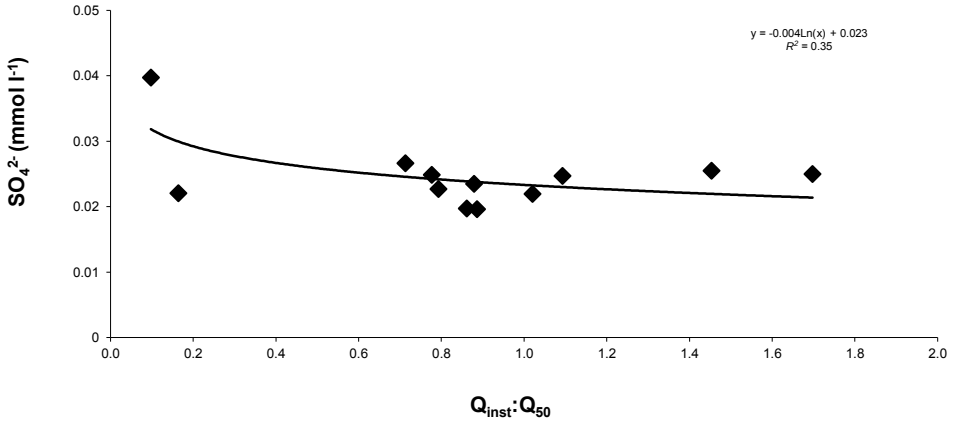


(b) **Changes in conductivity with discharge for the Elands (control) site.** Solid circles represent mainstream samples, for which a trend line was fitted, while open circles indicate values for isolated pools at natural low flows.

Appendix 5.2 Continued.

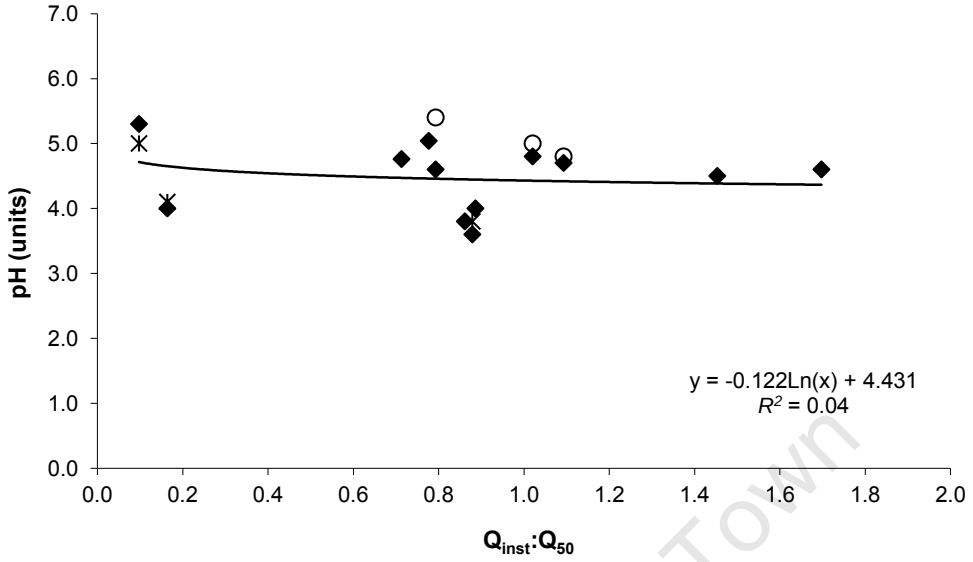


(c) **Changes in $[SO_4^{2-}]$ with discharge for the Elands site, for Dec-May.** Solid circles represent mainstream samples, for which a trend line was fitted.

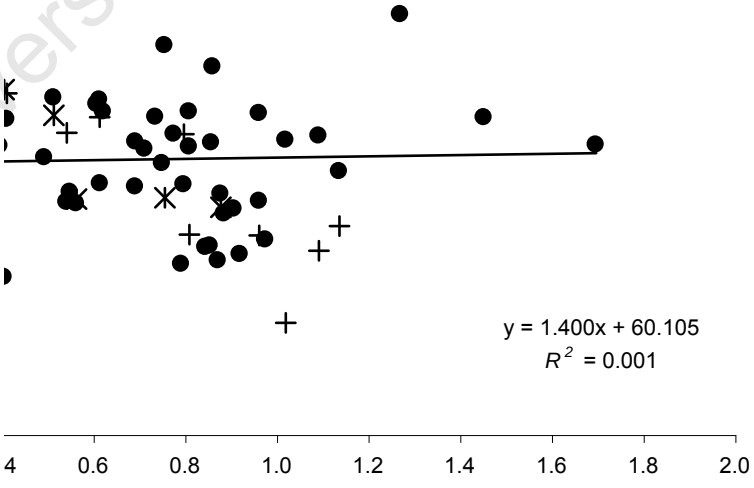


(d) **Changes in $[SO_4^{2-}]$ with discharge for the Riviersonderend site.** Solid diamonds represent mainstream samples, for which a trend line was fitted.

Appendix 5.2 Continued.

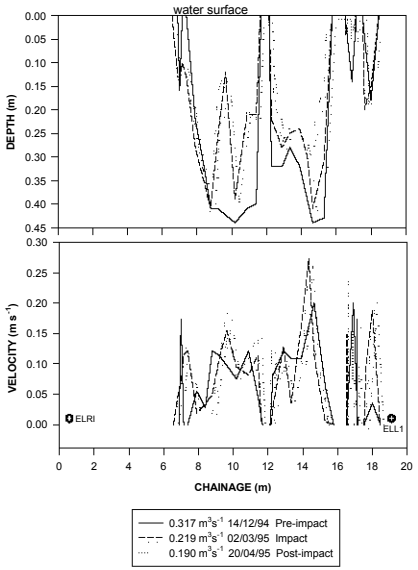


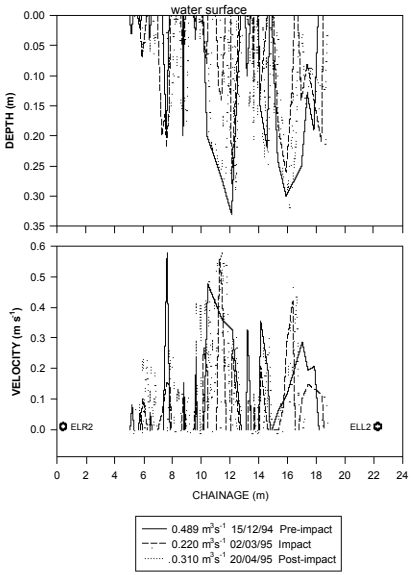
(e) **Changes in pH with discharge for the Riviersonderend site.** Solid diamonds represent mainstream samples, for which a trend line was fitted. Open circles and stars indicate values for isolated pools under natural and unnatural low flows, respectively.

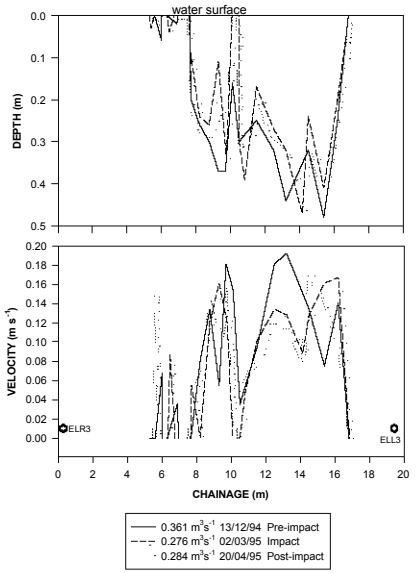


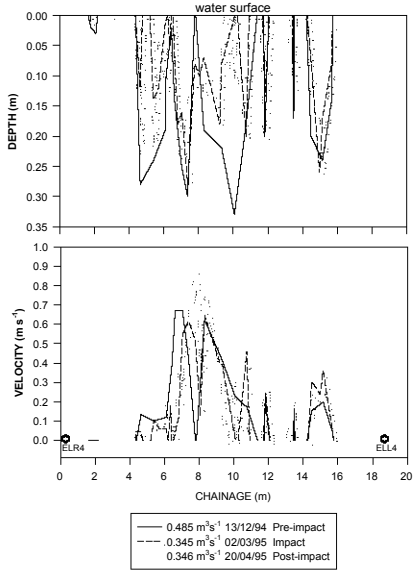
(f) **Relationship between dissolved oxygen in pool biotopes and discharge, for pooled data from all sites.** Solid circles represent mainstream samples, for which a trend line was fitted. Cross and star symbols indicate values for isolated (non-flowing) pools under natural and unnatural low flows, respectively.

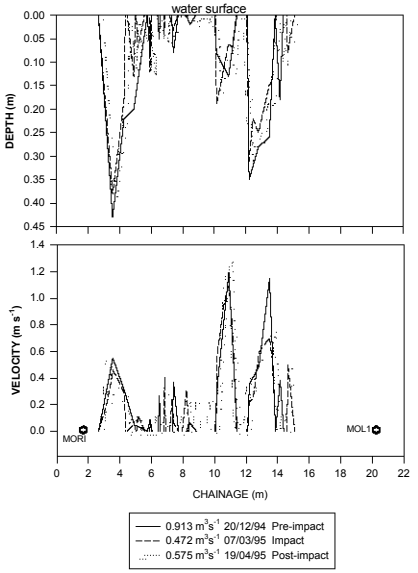
Appendix 6.1 Water depth and average velocity profiles for riffle and run cross-sections in the impact and control locations at the Elands (EL) and Molenaars (MO) sites, for three different discharges. Cross-section numbers as per Figures 3.2 and 3.3.

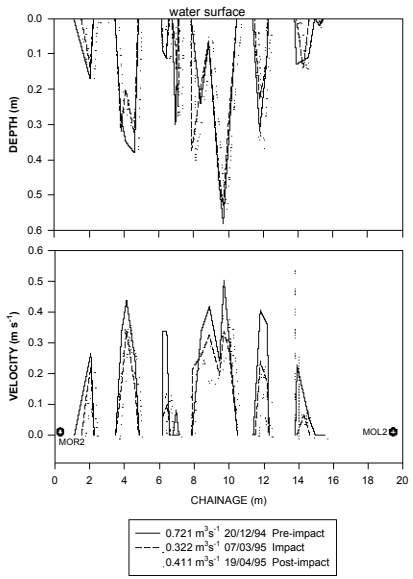


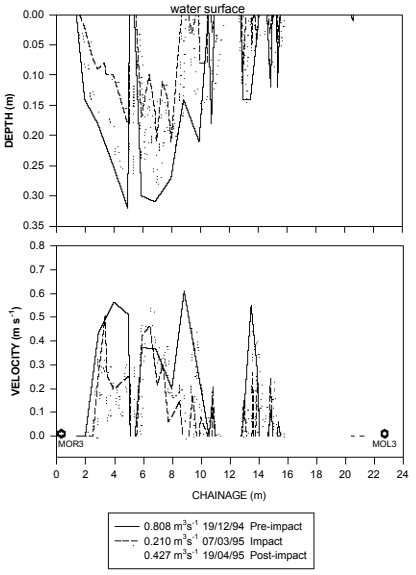


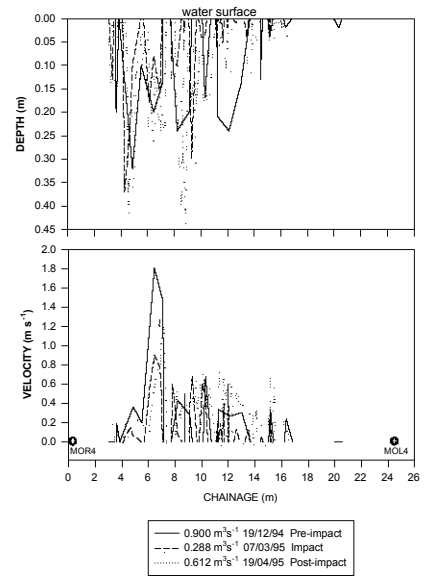




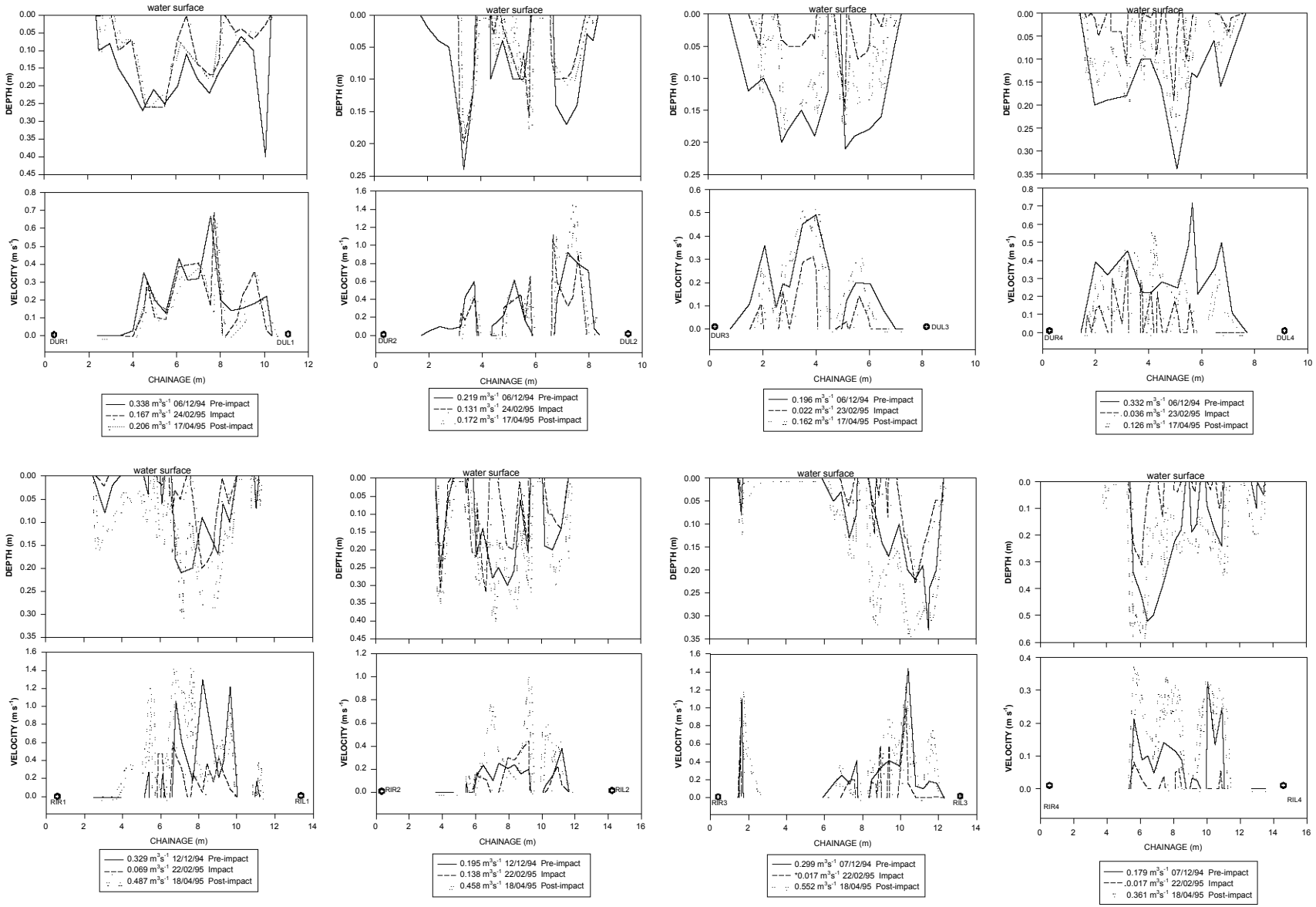




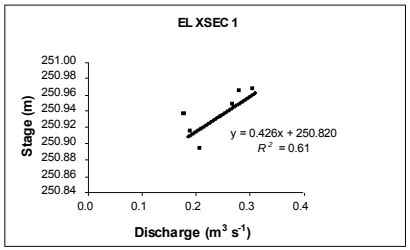


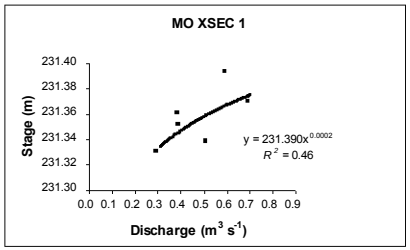


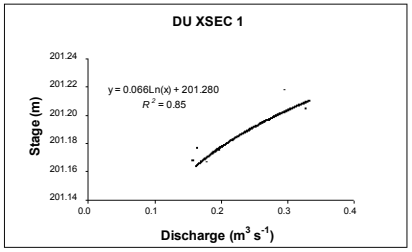
Appendix 6.1 Continued. Water depth and average velocity profiles for riffle and run cross-sections in the impact and control locations at the Du Toits (DU) and Riviersonderend (RI) sites, for three different discharges. Cross-section numbers as per Figures 3.4 and 3.5.

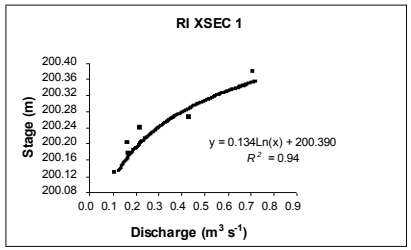


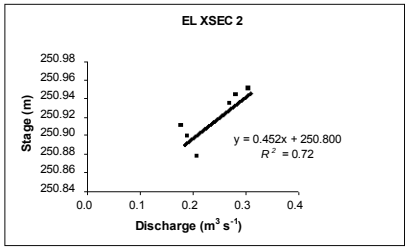
Appendix 6.2 Stage-discharge rating curves for cross-sections in site control and impact locations at each site. Cross-section numbers as per Figures 3.2-3.5. EL – Elands; Mo – Molenaars; DU – Du Toits; RI – Riviersonderend.

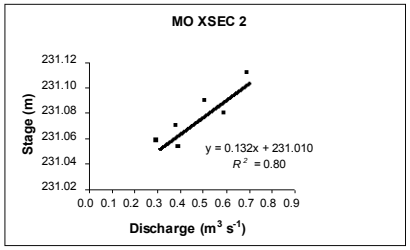


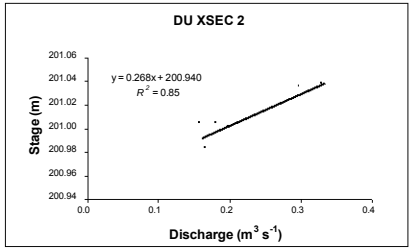


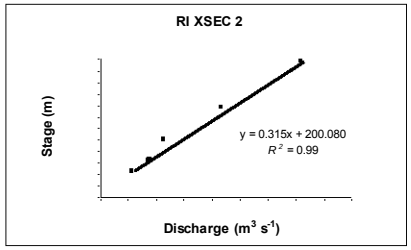


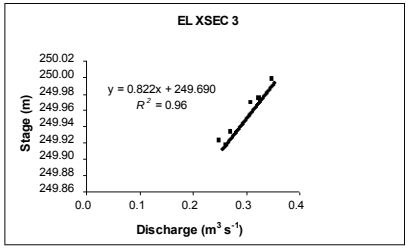


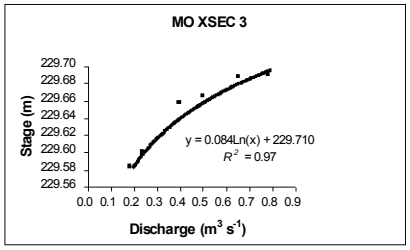


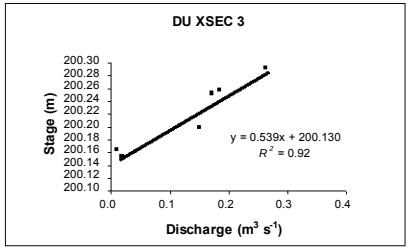


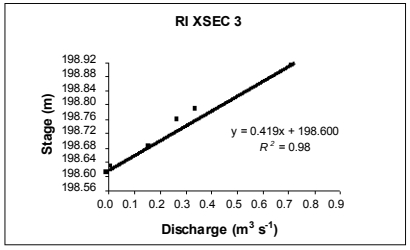


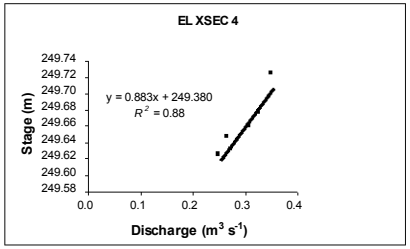


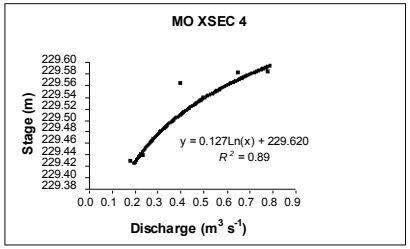


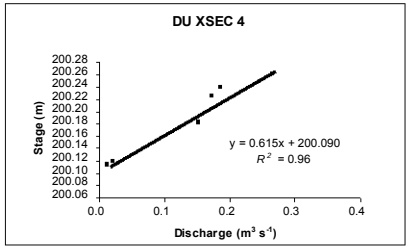


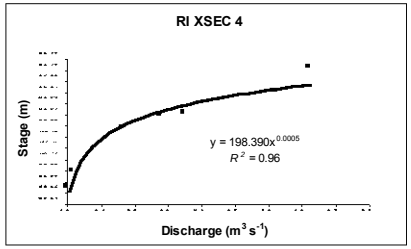












Appendix 6.3 Summary statistics for core and derived hydraulic indices used in the objective classification of biotopes, for the aggregate data set combining all sites and discharges. d_{50} - median particle size; Stand – standing water; Backw – backwater; Trans - transition; SD - standard deviation. * - Negative values for these variables are explained in the text.

CORE INDEX		Depth (m)					Mean column velocity (m s^{-1})					Near-bed velocity (m s^{-1})					Substratum d_{50} (m)				
BIOTOPE	***n***	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**
Stand	11	0.018	0.011	0.010	0.010	0.040	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.001	0.096	0.051	0.090	0.035	0.200
Backw	14	0.063	0.045	0.065	0.005	0.170	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.113	0.076	0.110	0.012	0.220
Pool	336	0.111	0.102	0.080	0.003	0.770	0.008	0.059	0.000	0.000	1.051	0.006	0.053	0.000	0.000	0.922	0.116	0.079	0.099	0.015	0.670
Pool/Run Trans	86	0.142	0.102	0.120	0.003	0.430	0.040	0.056	0.025	0.000	0.356	0.032	0.055	0.001	0.000	0.356	0.151	0.147	0.099	0.015	0.670
Trickle	11	0.024	0.016	0.030	0.001	0.040	0.048	0.086	0.001	0.000	0.287	0.048	0.086	0.001	0.000	0.287	0.203	0.101	0.180	0.070	0.380
Run	763	0.195	0.115	0.180	0.002	0.630	0.180	0.123	0.154	0.000	0.942	0.151	0.112	0.128	0.000	0.736	0.191	0.166	0.120	0.003	1.000
Riffle/Run Trans	124	0.132	0.078	0.125	0.001	0.340	0.296	0.135	0.286	0.042	0.637	0.262	0.132	0.253	0.000	0.637	0.174	0.146	0.110	0.003	0.600
Riffle	590	0.135	0.091	0.110	0.003	0.460	0.483	0.314	0.399	0.000	2.986	0.439	0.280	0.366	0.000	1.428	0.183	0.154	0.123	0.011	0.760

DERIVED INDEX		Velocity: depth ratio (s^{-1})					* Velocity shelter (m s^{-1})					Froude number (no units)				
BIOTOPE	***n***	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**
Stand	11	0.009	0.030	0.000	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.003
Backw	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pool	336	0.110	0.702	0.000	0.000	10.510	0.001	0.010	0.000	-0.080	0.129	0.009	0.062	0.000	0.000	1.061
Pool/Run Trans	86	0.662	2.208	0.144	0.000	19.200	0.008	0.027	0.000	-0.053	0.141	0.042	0.070	0.020	0.000	0.464
Trickle	11	16.020	34.592	0.200	0.000	95.667	0.000	0.000	0.000	0.000	0.000	0.248	0.523	0.005	0.000	1.673
Run	763	1.636	3.103	0.864	0.000	45.400	0.029	0.061	0.013	-0.139	0.622	0.155	0.134	0.119	0.000	1.159
Riffle/Run Trans	124	9.195	43.059	2.298	0.400	449.000	0.034	0.083	0.014	-0.297	0.371	0.364	0.483	0.269	0.044	4.533
Riffle	590	6.380	8.102	4.074	0.000	103.333	0.044	0.149	0.000	-0.330	1.676	0.507	0.353	0.434	0.000	2.104

Appendix 6.3 Continued.

DERIVED INDEX		Relative exposure/submergence (no units)					Turbulence index (m s^{-1})					Reynolds number (no units)				
BIOTOPE	***n***	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**
Stand	11	0.197	0.087	0.200	0.111	0.389	0.000	0.000	0.000	0.000	0.000	1	3	0	0	10
Backw	14	0.636	0.340	0.583	0.222	1.333	0.000	0.000	0.000	0.000	0.000	0	0	0	0	0
Pool	336	1.178	1.196	0.793	0.019	8.021	0.007	0.034	0.000	0.000	0.457	928	6121	0	0	105 100
Pool/Run Trans	86	1.846	2.492	0.992	0.004	16.000	0.098	0.390	0.017	0.000	3.552	6780	12 972	2315	0	88 800
Trickle	11	0.148	0.161	0.108	0.006	0.571	0.003	0.004	0.000	0.000	0.012	588	1132	40	0	3800
Run	763	1.990	2.975	1.200	0.005	36.667	0.388	0.955	0.176	0.000	14.500	36 003	38 709	25 380	0	324 450
Riffle/Run Trans	124	1.556	3.696	0.959	0.003	40.000	0.458	1.092	0.249	0.001	11.720	39 562	31 718	31 985	449	153 660
Riffle	590	1.234	1.381	0.774	0.005	12.727	0.591	0.898	0.325	0.000	15.262	65 437	67 479	45 560	0	686 780

DERIVED INDEX		Relative roughness (no units)					* Shear velocity (m s^{-1})					* Roughness Reynolds number (no units)				
BIOTOPE	***n***	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**	**Mean**	**SD**	**Median**	**Min**	**Max**
Stand	11	6.0	2.5	5.0	2.6	9.0	0.0001	0.0004	0.0000	0.0000	0.0014	11	38	0	0	125
Backw	14	2.1	1.1	1.8	0.8	4.5	0.0000	0.0000	0.0000	0.0000	0.0000	0	0	0	0	0
Pool	334	3.2	6.1	1.3	0.1	52.0	0.0022	0.0178	0.0000	-0.0140	0.2548	635	6490	0	-9408	98 950
Pool/Run Trans	86	4.6	24.4	1.0	0.1	224.0	0.0086	0.0189	0.0030	-0.0066	0.1539	2147	8903	227	-3678	80 033
Trickle	11	28.8	51.4	9.3	1.8	180.0	-0.0066	0.0726	0.0000	-0.1728	0.1462	2299	18 086	0	-15 895	54 079
Run	763	2.5	11.7	0.8	0.0	215.0	0.0299	0.0499	0.0234	-0.6990	0.5551	6694	21 660	2926	-286 574	212 171
Riffle/Run Trans	124	6.2	29.4	1.0	0.0	310.0	0.0444	0.1587	0.0490	-1.4892	0.6707	12 173	39 562	5317	-95 306	348 739
Riffle	590	3.2	10.7	1.3	0.1	200.0	0.1077	0.3850	0.0770	-3.1687	6.7062	31 146	249 590	9877	-1147 729	5096 676

Appendix 7.1 Benthic macroinvertebrate families and higher taxa recorded (●) at the study sites. u - absent from uppermost stones, but recorded from the underlying substratum.

TAXON	ELANDS	MOLENAARS	DU TOITS	RIVIERSONDEREND
ACARINA	●	●	●	●
CNIDARIA	●	●		
COLEOPTERA				
Dryopidae	●	●		●
Dytiscidae		●	●	
Elmidae	●	●	●	●
Gyrinidae	●	●	●	●
Helodidae	●	●	●	●
Hydraenidae	●	●	●	●
Hydrophilidae	●			●
Limnichidae	●	●	●	●
COLLEMBOLA	●	●	●	
DIPTERA				
Blepharoceridae	●	●		
Ceratopogonidae	●	●	●	●
Chironomidae	●	●	●	●
Culicidae		●	●	
Dixidae	●	●	u	
Empididae	●	●	●	●
Athericidae	●	●	●	●
Simuliidae	●	●	●	●
Tipulidae	●	●	●	●
Psychodidae			●	
EPHEMEROPTERA				
Baetidae	●	●	●	●
Caenidae	●	●	●	
Teloganodidae	●	●	●	●
Heptageniidae	●	●	●	
Leptophlebiidae	●	●	●	●
HEMIPTERA				
Corixidae	●	●	●	●
Mesoveliidae	●			
Naucoridae			●	
Notonectidae	●	●	●	●
Veliidae	●		●	●
Hebridae	●			
LEPIDOPTERA				
Pyraustidae	●	●		●
MEGALOPTERA				
Corydalidae	●	●	●	●
NEMATODA	●	●	●	●
ODONATA				
Coenagrionidae	●			●
Aeshnidae	●	●	●	●
Gomphidae		●	u	●
Libellulidae		●	●	●
OLIGOCHAETA	●	●	●	●
PLATYHELMINTHES	●	●	●	u
PLECOPTERA				
Notonemouridae	●	●	●	●

Appendix 7.1 Continued.

TAXON	ELANDS	MOLENAARS	DU TOITS	RIVIERSONDEREND
TRICHOPTERA				
Barbarochthonidae	●			●
Ecnomidae	●	●	●	●
Glossosomatidae	●	●	●	
Hydropsychidae	●	●	●	●
Hydroptilidae	●	●	●	●
Leptoceridae	●	●	●	●
Petrothrincidae			●	
Philopotamidae	●	●	●	●
Polycentropodidae	●	●		
Sericostomatidae			●	●
THYSANOPTERA				
*Thripidae	●	●	●	●

* Some members of the family known to inhabit damp substrata, aquatic macrophtes, etc.

Appendix 7.2 Results of a SIMPER analysis comparing average family and higher taxon abundances (0.1 m^{-2}) among site pairs. $\bar{\delta}_i$ = the contribution of the *i*th taxon to the overall average dissimilarity ($\bar{\delta}$) between sites, expressed as a cumulative percentage ($\Sigma \bar{\delta}_i$ %). Data are derived from whole stones (invertebrates from underlying substrata excluded). Taxa are listed from greatest to least contribution to dissimilarity (cutoff at ≤ 50%), with the higher abundance for each taxon between groups indicated in bold.

$\bar{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma \bar{\delta}_i$ %
EL and MO = 29.63%	**EL**	**MO**				
Simuliidae	17.63	**88.33**	2.28	1.70	7.71	7.71
Baetidae	197.20	**385.40**	1.59	1.38	5.37	13.08
Chironomidae	57.10	**169.32**	1.42	1.49	4.80	17.88
Oligochaeta	4.11	**5.86**	0.94	1.19	3.16	21.04
Teloganodidae	**47.95**	21.85	0.92	1.55	3.11	24.16
Hydraenidae	0.17	**0.71**	0.90	1.29	3.05	27.21
Ceratopogonidae	0.28	**0.56**	0.88	1.53	2.98	30.19
Acarina	5.33	**16.34**	0.87	1.96	2.93	33.12
Corixidae	0.41	**0.59**	0.84	1.21	2.82	35.94
Limnichidae	0.22	**0.38**	0.79	1.41	2.66	38.60
Caenidae	0.12	**0.72**	0.76	0.97	2.56	41.16
Hydropsychidae	4.46	**8.77**	0.72	1.57	2.44	43.61
Helodidae	**0.32**	0.12	0.67	1.14	2.28	45.88
Thripidae	0.15	**0.27**	0.67	1.17	2.27	48.15
Hydroptilidae	0.58	**0.69**	0.65	1.24	2.20	50.35
EL and DU = 39.40%	**EL**	**DU**				
Simuliidae	17.63	**237.97**	2.96	1.58	7.50	7.50
Chironomidae	57.10	**269.33**	2.02	2.24	5.13	12.63
Caenidae	0.12	**7.37**	1.91	2.13	4.84	17.47
Notonemouridae	0.32	**7.02**	1.81	2.52	4.60	22.07
Leptoceridae	1.11	**25.04**	1.73	2.60	4.40	26.47
Heptageniidae	**7.17**	0.74	1.66	1.82	4.22	30.69
Hydropsychidae	**4.46**	0.21	1.56	2.19	3.97	34.66
Hydroptilidae	0.58	**10.34**	1.37	1.98	3.47	38.12
Teloganodidae	**47.95**	11.87	1.31	1.97	3.32	41.44
Baetidae	**197.20**	138.05	1.12	1.49	2.83	44.27
Acarina	5.33	**29.38**	1.09	1.53	2.76	47.03
Athericidae	0.28	**2.56**	1.01	1.66	2.56	49.59
Empididae	0.16	**0.99**	1.00	1.54	2.55	52.14
MO and RI = 38.73%	**MO**	**RI**				
Baetidae	**385.40**	37.89	3.35	2.02	8.66	8.66
Heptageniidae	**8.71**	0.00	2.92	7.93	7.54	16.20
Simuliidae	**88.33**	7.35	2.25	1.65	5.82	22.02
Hydropsychidae	**8.77**	0.32	2.16	1.99	5.57	27.59
Philopotamidae	**1.35**	0.10	1.40	2.10	3.62	31.20
Teloganodidae	**21.85**	3.27	1.39	2.51	3.59	34.80
Leptophlebiidae	**9.32**	1.44	1.25	1.74	3.23	38.02
Hydroptilidae	0.69	**3.65**	1.13	1.31	2.91	40.93
Hydraenidae	**0.71**	0.03	1.08	1.41	2.79	43.72
Chironomidae	**169.32**	155.04	1.07	1.38	2.76	46.48
Limnichidae	**0.38**	0.00	1.05	1.88	2.72	49.21
Ceratopogonidae	**0.56**	0.13	1.00	1.55	2.58	51.78

Appendix 7.2 Continued.

$\bar{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma\bar{\delta}_i$ %
MO and DU = 33.06%	**MO**	**DU**				
Notonemouridae	0.08	**7.02**	1.83	3.93	5.53	5.53
Hydropsychidae	**8.77**	0.21	1.76	2.19	5.32	10.85
Heptageniidae	**8.71**	0.74	1.66	1.97	5.02	15.87
Simuliidae	88.33	**237.97**	1.58	1.23	4.77	20.64
Baetidae	**385.40**	138.05	1.51	1.40	4.56	25.20
Caenidae	0.72	**7.37**	1.46	1.67	4.41	29.61
Hydroptilidae	0.69	**10.34**	1.40	1.83	4.25	33.86
Leptoceridae	2.13	**25.04**	1.35	2.15	4.08	37.94
Chironomidae	169.32	**269.33**	1.03	1.42	3.12	41.06
Empididae	0.04	**0.99**	1.00	1.72	3.04	44.10
Philopotamidae	**1.35**	0.30	0.81	1.35	2.44	46.53
Helodidae	0.12	**0.96**	0.80	1.38	2.43	48.97
Oligochaeta	5.86	**11.45**	0.80	1.12	2.43	51.39
EL and RI = 38.10%	**EL**	**RI**				
Heptageniidae	**7.17**	0.00	3.05	6.92	8.00	8.00
Baetidae	**197.20**	37.89	2.45	1.69	6.44	14.44
Teloganodidae	**47.95**	3.27	2.37	2.74	6.23	20.67
Hydropsychidae	**4.46**	0.32	1.94	1.87	5.09	25.76
Chironomidae	57.10	**155.04**	1.60	1.63	4.21	29.97
Philopotamidae	**1.33**	0.10	1.45	1.85	3.80	33.77
Simuliidae	**17.63**	7.35	1.20	1.10	3.16	36.93
Leptoceridae	1.11	**7.68**	1.10	1.50	2.90	39.83
Elmidae	4.61	**18.53**	1.08	1.52	2.84	42.67
Hydroptilidae	0.58	**3.65**	1.01	1.23	2.66	45.33
Notonemouridae	0.32	**0.59**	1.01	1.43	2.65	47.98
Corixidae	0.41	**0.42**	0.91	1.01	2.39	50.37
DU and RI = 35.36%	**DU**	**RI**				
Simuliidae	**237.97**	7.35	3.04	1.55	8.60	8.60
Caenidae	**7.37**	0.00	2.28	2.52	6.46	15.06
Baetidae	**138.05**	37.89	1.73	1.55	4.90	19.96
Notonemouridae	**7.02**	0.59	1.44	2.02	4.06	24.02
Chironomidae	**269.33**	155.04	1.18	1.39	3.34	27.37
Leptoceridae	**25.04**	7.68	1.18	1.40	3.34	30.70
Leptophlebiidae	**10.59**	1.44	1.14	1.42	3.22	33.92
Empididae	**0.99**	0.05	1.08	1.62	3.06	36.98
Ceratopogonidae	**1.64**	0.13	1.06	1.18	2.99	39.97
Helodidae	**0.96**	0.08	1.06	1.51	2.99	42.95
Hydraenidae	**0.59**	0.03	1.01	1.50	2.84	45.80
Acarina	**29.38**	10.61	0.99	1.34	2.80	48.60
Ephemeroptera (juveniles)	**1.10**	0.13	0.92	1.11	2.60	51.20

Appendix 7.3 Results of SIMPER analyses comparing average family and higher taxon abundances (0.1 m^{-2}) among biotopes for individual sites. (a) Elands. $\overline{\delta}_i$ = the contribution of the *i*th taxon to the overall average dissimilarity ($\overline{\delta}$) between biotopes, expressed as a cumulative percentage ($\Sigma \overline{\delta}_i$ %). Data are derived from whole stones (invertebrates from underlying substrata were excluded). Taxa are listed from greatest to least contribution to dissimilarity (cutoff at ≤ 50%), with the higher abundance for each taxon between groups indicated in bold.

$\overline{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma \overline{\delta}_i$ %
Riffle and Run = 39.03%	**Riffle**	**Run**				
Simuliidae	**49.39**	2.66	2.88	1.29	7.37	7.37
Baetidae	**309.91**	125.37	2.26	1.30	5.80	13.17
Hydropsychidae	**11.30**	1.92	2.24	1.42	5.74	18.90
Chironomidae	**121.99**	37.39	2.13	1.34	5.45	24.36
Oligochaeta	**9.90**	1.54	1.95	1.29	4.99	29.34
Philopotamidae	**3.50**	0.38	1.94	1.56	4.97	34.32
Acarina	**12.28**	2.82	1.84	1.34	4.73	39.04
Leptophlebiidae	**5.16**	3.00	1.55	1.23	3.96	43.01
Leptoceridae	0.46	**1.18**	1.42	1.31	3.64	46.65
Hydroptilidae	**1.45**	0.28	1.37	1.32	3.52	50.17
Riffle and Pool = 45.50%	**Riffle**	**Pool**				
Simuliidae	**49.39**	0.86	3.42	1.51	7.52	7.52
Hydropsychidae	**11.30**	0.16	3.35	3.07	7.35	14.87
Chironomidae	**121.99**	11.94	2.91	2.57	6.40	21.27
Acarina	**12.28**	0.90	2.65	1.88	5.82	27.09
Baetidae	**309.91**	156.33	2.38	1.41	5.24	32.33
Philopotamidae	**3.50**	0.12	2.12	1.76	4.65	36.99
Oligochaeta	**9.90**	0.89	2.08	1.40	4.57	41.56
Teloganodidae	27.56	**76.13**	1.77	1.39	3.88	45.44
Hydroptilidae	**1.45**	0.00	1.73	1.59	3.81	49.25
Leptoceridae	0.46	**1.70**	1.66	1.43	3.65	52.90
Run and Pool = 37.16%	**Run**	**Pool**				
Baetidae	125.37	**156.33**	2.26	1.16	6.08	6.08
Teloganodidae	40.16	**76.13**	2.17	1.27	5.84	11.93
Leptophlebiidae	3.00	**6.13**	2.00	1.07	5.38	17.31
Simuliidae	**2.66**	0.86	1.95	1.06	5.24	22.55
Hydropsychidae	**1.92**	0.16	1.87	1.19	5.02	27.58
Acarina	**2.82**	0.90	1.86	1.17	5.00	32.57
Chironomidae	**37.39**	11.94	1.85	1.69	4.99	37.56
Oligochaeta	**1.54**	0.89	1.81	1.19	4.88	42.44
Heptageniidae	**10.53**	3.80	1.73	1.27	4.65	47.09
Leptoceridae	1.18	**1.70**	1.55	1.22	4.16	51.25

Appendix 7.3 Continued. (b) Molenaars.

$\overline{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\overline{\delta}_i$ %
Riffle and Run = 34.37%	**Riffle**	**Run**				
Simuliidae	**256.87**	7.32	3.51	2.08	10.22	10.22
Baetidae	**683.16**	344.09	2.23	1.35	6.48	16.70
Philopotamidae	**3.33**	0.58	1.86	2.34	5.41	22.11
Hydropsychidae	**20.86**	5.32	1.77	1.37	5.14	27.25
Acarina	**37.93**	10.57	1.67	1.43	4.87	32.12
Chironomidae	**300.71**	190.85	1.62	1.35	4.73	36.84
Leptoceridae	0.86	**4.21**	1.36	1.37	3.95	40.80
Oligochaeta	6.71	**8.31**	1.23	1.24	3.57	44.36
Teloganodidae	10.10	**33.96**	1.17	1.59	3.41	47.77
Hydraenidae	**1.74**	0.25	1.06	1.14	3.10	50.87
Riffle and Pool = 48.94%	**Riffle**	**Pool**				
Simuliidae	**256.87**	0.79	5.89	2.90	12.03	12.03
Chironomidae	**300.71**	16.39	4.24	2.88	8.67	20.70
Acarina	**37.93**	0.53	3.51	2.51	7.18	27.87
Hydropsychidae	**20.86**	0.12	3.47	2.80	7.10	34.97
Baetidae	**683.16**	128.97	3.40	1.54	6.95	41.93
Philopotamidae	**3.33**	0.13	2.10	2.20	4.29	46.22
Oligochaeta	**6.71**	2.54	1.62	1.38	3.32	49.54
Leptophlebiidae	**11.80**	2.53	1.55	1.49	3.16	52.70
Run and Pool = 38.13%	**Run**	**Pool**				
Chironomidae	**190.85**	16.39	3.56	1.86	9.33	9.33
Baetidae	**344.09**	128.97	2.53	1.44	6.63	15.96
Acarina	**10.57**	0.53	2.32	1.47	6.08	22.04
Hydropsychidae	**5.32**	0.12	2.20	1.36	5.76	27.81
Simuliidae	**7.32**	0.79	2.11	1.53	5.53	33.33
Leptophlebiidae	**13.63**	2.53	1.86	1.44	4.87	38.20
Oligochaeta	**8.31**	2.54	1.81	1.28	4.74	42.94
Athericidae	**1.21**	0.07	1.80	1.73	4.72	47.66
Teloganodidae	**33.96**	21.49	1.52	0.97	3.99	51.66

Appendix 7.3 Continued. (c) Du Toits.

$\overline{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\overline{\delta}_i$ %
Riffle and Run = 32.25%	**Riffle**	**Run**				
Simuliidae	**696.43**	15.41	4.07	1.50	12.61	12.61
Baetidae	**267.07**	58.52	2.00	1.65	6.19	18.80
Chironomidae	**512.49**	206.85	1.86	1.50	5.77	24.56
Empididae	**2.68**	0.28	1.34	1.51	4.14	28.71
Teloganodidae	3.28	**14.28**	1.31	1.42	4.05	32.75
Acarina	**46.47**	34.81	1.27	1.48	3.93	36.68
Elmidae	**21.60**	4.53	1.24	1.28	3.84	40.52
Caenidae	0.61	**3.06**	1.22	1.25	3.79	44.31
Leptophlebiidae	4.41	**8.25**	1.14	1.15	3.52	47.83
Hydraenidae	**1.47**	0.15	1.04	1.15	3.21	51.04
Riffle and Pool = 43.54%	**Riffle**	**Pool**				
Simuliidae	**696.43**	2.07	6.19	1.89	14.21	14.21
Chironomidae	**512.49**	88.65	3.15	2.06	7.23	21.44
Baetidae	**267.07**	88.56	2.73	1.79	6.27	27.71
Caenidae	0.61	**18.45**	2.39	1.71	5.49	33.21
Acarina	**46.47**	6.86	2.02	1.51	4.64	37.84
Leptoceridae	5.79	**56.76**	1.95	1.46	4.48	42.33
Elmidae	**21.60**	2.84	1.79	1.46	4.12	46.44
Empididae	**2.68**	0.00	1.71	1.89	3.93	50.37
Run and Pool = 34.02%	**Run**	**Pool**				
Simuliidae	**15.41**	2.07	2.10	1.39	6.19	6.19
Caenidae	3.06	**18.45**	2.00	1.25	5.87	12.06
Chironomidae	**206.85**	88.65	1.89	1.53	5.54	17.60
Acarina	**34.81**	6.86	1.80	1.20	5.29	22.90
Athericidae	**3.21**	0.77	1.53	1.50	4.50	27.40
Baetidae	58.52	**88.56**	1.41	1.18	4.14	31.54
Leptoceridae	12.59	**56.76**	1.40	1.27	4.12	35.66
Ceratopogonidae	1.27	**3.22**	1.38	1.07	4.06	39.72
Oligochaeta	**8.62**	5.70	1.33	1.14	3.92	43.64
Hydroptilidae	**12.56**	3.12	1.29	1.17	3.80	47.44
Teloganodidae	14.28	**18.04**	1.17	0.99	3.43	50.87

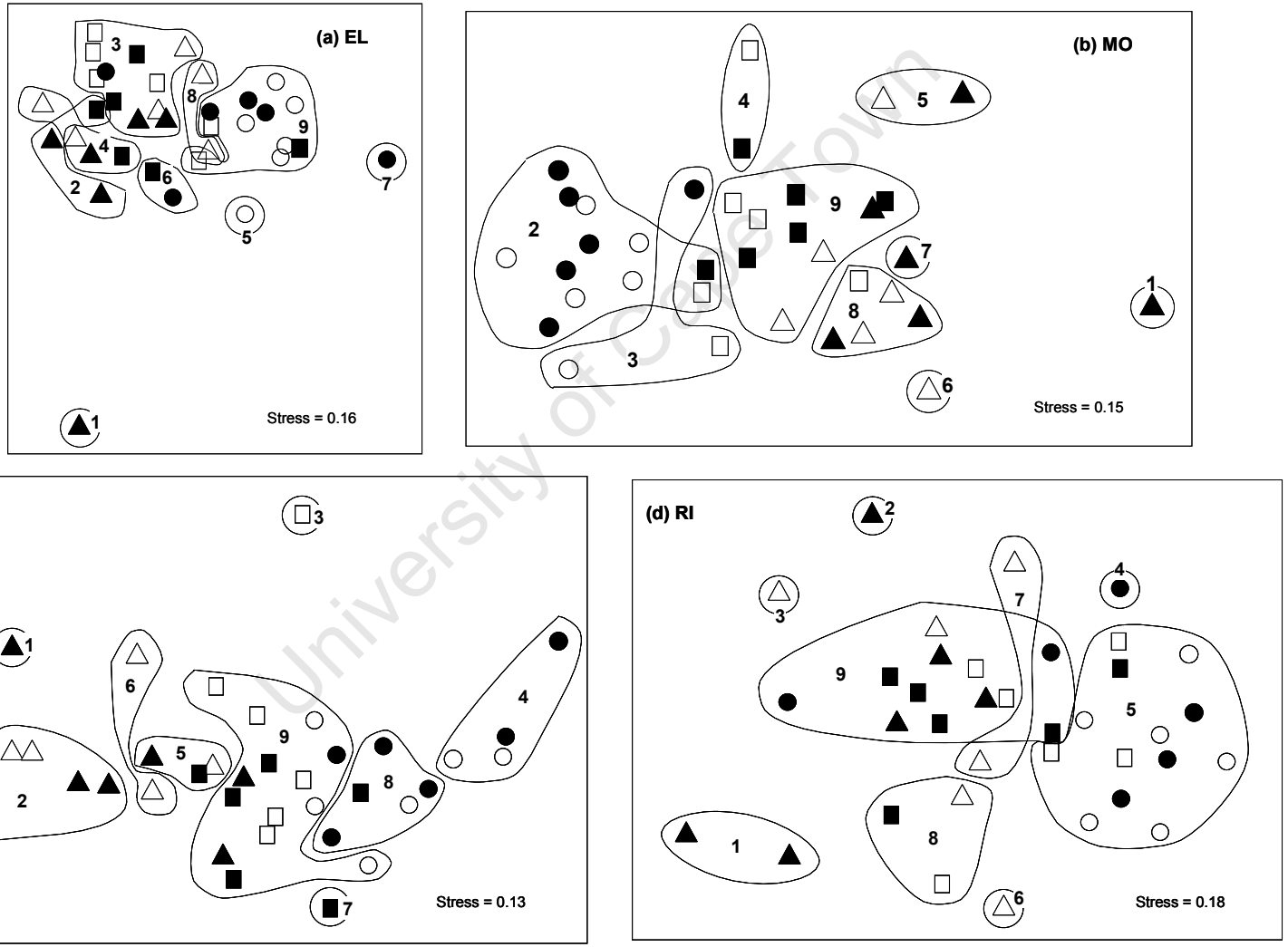
Appendix 7.3 Continued. (d) Riviersonderend.

$\overline{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ %	$\Sigma\overline{\delta}_i$ %
Riffle and Run = 34.13%	**Riffle**	**Run**				
Chironomidae	**169.42**	103.57	2.36	1.33	6.91	6.91
Baetidae	**83.82**	22.68	2.32	1.34	6.81	13.72
Elmidae	**34.72**	16.87	2.31	1.13	6.76	20.48
Oligochaeta	**6.10**	1.40	2.04	1.25	5.97	26.46
Simuliidae	**19.77**	1.91	2.01	1.64	5.88	32.34
Notonemouridae	**1.59**	0.19	1.89	1.48	5.54	37.88
Teloganodidae	1.19	**3.39**	1.87	1.16	5.47	43.35
Leptoceridae	1.81	**4.89**	1.68	1.10	4.94	48.29
Leptophlebiidae	**1.15**	1.06	1.61	1.23	4.71	52.99
Riffle and Pool = 42.60%	**Riffle**	**Pool**				
Simuliidae	**19.77**	0.37	4.02	2.29	9.44	9.44
Baetidae	**83.82**	7.18	3.30	1.57	7.75	17.19
Elmidae	**34.72**	4.00	3.07	1.33	7.21	24.39
Leptoceridae	1.81	**16.34**	2.58	1.30	6.05	30.45
Oligochaeta	**6.10**	1.58	2.29	1.38	5.36	35.81
Notonemouridae	**1.59**	0.00	2.16	1.64	5.06	40.87
Teloganodidae	1.19	**5.24**	2.08	1.12	4.87	45.74
Athericidae	**1.92**	0.63	2.05	1.40	4.82	50.56
Run and Pool = 37.05%	**Run**	**Pool**				
Chironomidae	103.57	**192.13**	2.99	1.27	8.06	8.06
Leptoceridae	4.89	**16.34**	2.73	1.32	7.38	15.44
Simuliidae	**1.91**	0.37	2.57	1.66	6.94	22.38
Elmidae	**16.87**	4.00	2.56	1.06	6.91	29.29
Athericidae	**1.13**	0.63	2.20	1.44	5.93	35.23
Hydroptilidae	**4.96**	1.44	2.18	1.38	5.89	41.11
Oligochaeta	1.40	**1.58**	2.13	1.23	5.74	46.85
Baetidae	**22.68**	7.18	2.10	1.36	5.68	52.53

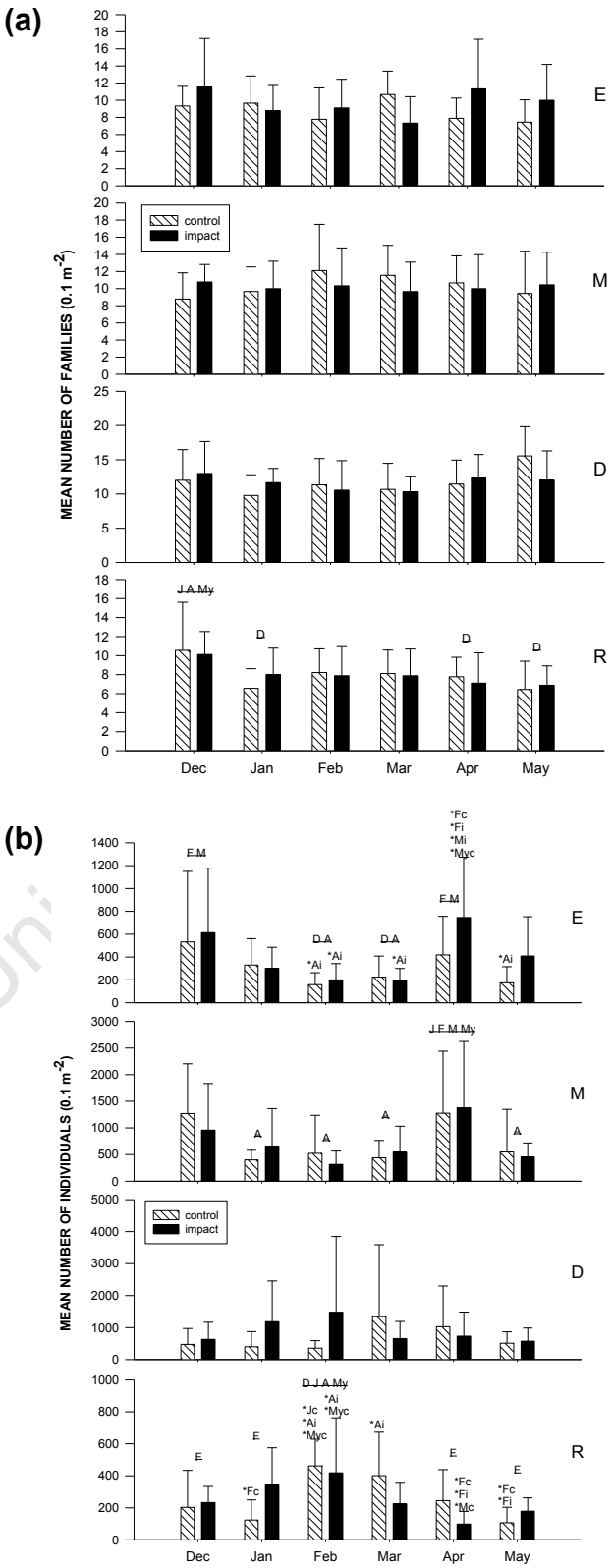
Appendix 7.4 Results of a SIMPER analysis comparing invertebrate assemblages from December and May for each site.

$\bar{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL TAXA	AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma \bar{\delta}_i$ %
Elands						
Dec and May = 42.14%	**Dec**	**May**				
Simuliidae	**82.68**	1.16	3.66	1.38	8.69	8.69
Baetidae	**379.48**	151.06	2.92	1.41	6.93	15.63
Leptophlebiidae	3.45	**8.92**	2.30	1.26	5.46	21.08
Teloganodidae	15.35	**43.73**	2.26	1.41	5.37	26.46
Hydropsychidae	**8.78**	1.92	2.19	1.36	5.20	31.65
Oligochaeta	8.05	**9.08**	2.05	1.35	4.87	36.52
Acarina	**9.25**	1.89	1.98	1.23	4.70	41.22
Chironomidae	48.29	**55.08**	1.83	1.41	4.35	45.57
Heptageniidae	3.18	**6.54**	1.79	1.19	4.25	49.82
Philopotamidae	**3.47**	1.66	1.72	1.19	4.07	53.90
Molenaars						
Dec and May = 40.48%	**Dec**	**May**				
Baetidae	**761.19**	221.38	2.94	2.38	7.27	7.27
Simuliidae	21.83	**115.21**	2.86	1.35	7.06	14.33
Hydropsychidae	**15.82**	0.40	2.58	1.52	6.38	20.71
Acarina	**20.50**	2.29	2.45	1.51	6.05	26.77
Chironomidae	**226.98**	110.87	2.03	1.34	5.01	31.77
Oligochaeta	**18.84**	3.19	1.93	1.28	4.78	36.55
Teloganodidae	13.95	**20.31**	1.84	0.99	4.55	41.10
Collembola	0.00	**0.99**	1.75	1.79	4.32	45.42
Philopotamidae	**3.30**	0.41	1.63	1.27	4.03	49.45
Leptophlebiidae	7.37	**7.41**	1.60	1.08	3.95	53.40
Du Toits						
Dec and May = 33.71%	**Dec**	**May**				
Teloganodidae	1.75	**10.60**	1.78	1.65	5.28	5.28
Baetidae	**217.38**	89.38	1.74	1.39	5.17	10.46
Chironomidae	168.45	**314.23**	1.67	1.34	4.96	15.42
Caenidae	**2.02**	1.97	1.64	1.85	4.88	20.29
Ephemeroptera (juveniles)	**4.06**	0.00	1.58	1.31	4.70	24.99
Heptageniidae	0.00	**1.37**	1.55	2.01	4.61	29.60
Simuliidae	**37.65**	17.37	1.51	1.34	4.48	34.08
Helodidae	0.23	**3.85**	1.38	1.46	4.10	38.18
Collembola	0.20	**2.22**	1.34	1.28	3.96	42.14
Leptoceridae	**54.31**	13.97	1.18	1.06	3.51	45.65
Empididae	**1.35**	0.77	1.08	1.36	3.19	48.84
Oligochaeta	9.91	**28.08**	1.05	1.17	3.11	51.95
Riviersonderend						
Dec and May = 40.99%	**Dec**	**May**				
Leptoceridae	**21.07**	1.35	3.59	1.35	8.77	8.77
Hydroptilidae	0.73	**7.26**	3.11	1.45	7.58	16.35
Athericidae	**3.41**	0.15	2.86	2.10	6.99	23.34
Teloganodidae	2.45	**3.57**	2.79	2.30	6.82	30.16
Simuliidae	**11.83**	1.26	2.43	1.40	5.93	36.09
Elmidae	4.55	**20.37**	2.36	1.46	5.76	41.85
Oligochaeta	1.91	**2.60**	2.23	1.32	5.44	47.29
Baetidae	**41.47**	9.20	2.12	1.39	5.17	52.45

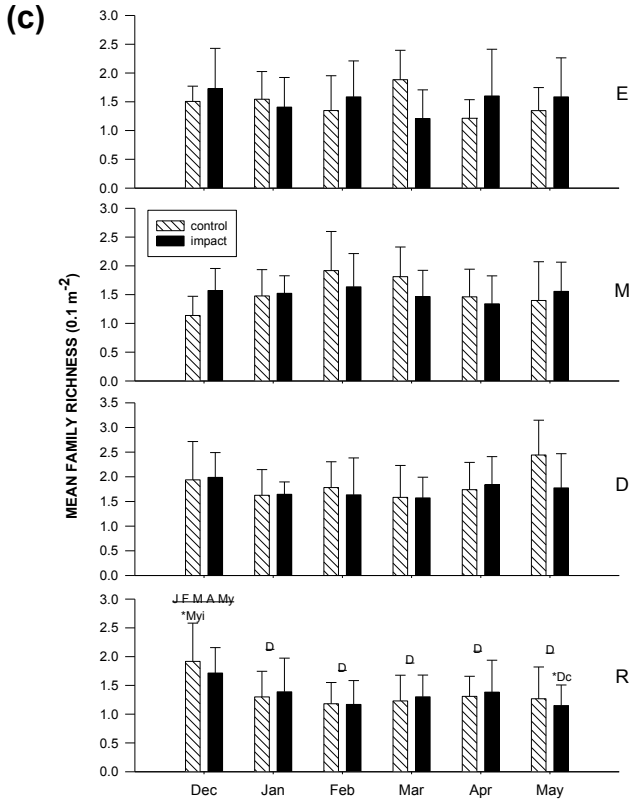
Appendix 7.5 **Ordination plots, based on the same similarity matrices as Figures 7.6-7.9, of invertebrate samples from different biotopes (family abundances 0.1 m^{-2}) collected from the control (C) and impact (I) locations during the impact phase, for the sites.** (a) EL – Elands; (b) MO – Molenaars; (c) Du – Du Toits; (d) RI – Riviersonderend. Main groups from the dendrogram, with corresponding numbers, are superimposed (dashed line polygons). Control location (open symbols) and impact location (solid symbols). Riffles (circles), runs (squares) and pools (triangles).

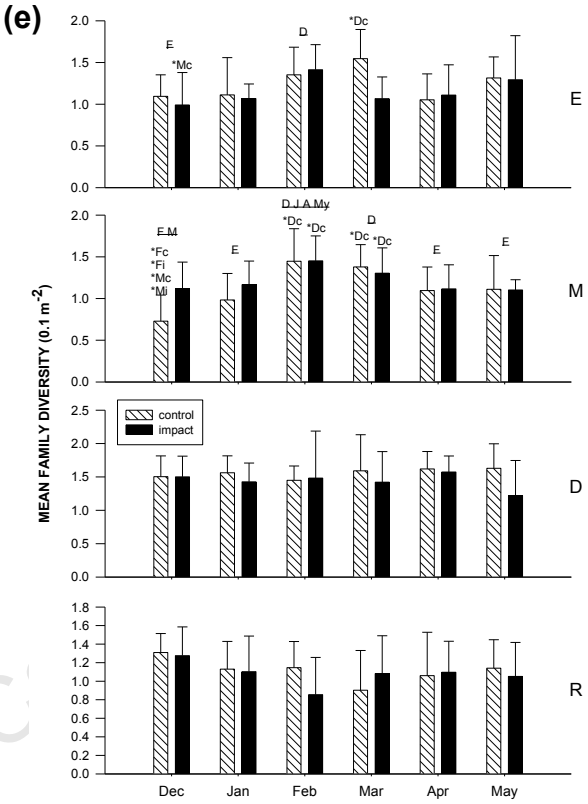


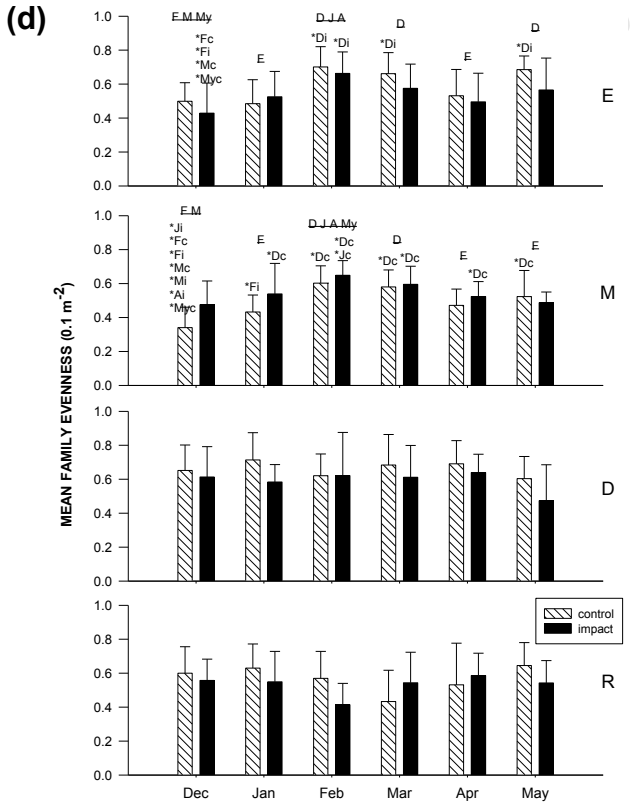
Appendix 7.6 **Time series plots of diversity indices for control and impact locations at individual sites over the study period. (a) Mean numbers of families. (b) Mean total numbers of individuals.** E - Elands; M - Molenaars; D - Du Toits; R - Riviersonderend. Error bars represent SDs. Significant differences among months underscored: D (Dec) to My (May). Significant differences between location pairs are indicated by an asterisk preceding the corresponding month (D-My) and location (c, i) (e.g. *Ai - mean value for the location indicated differs significantly from that of the April impact location). Note different axis scales.



Appendix 7.6 Continued. Time series plots of diversity indices for control and impact locations at individual sites over the study period. (c) Mean family richness. (d) Mean family evenness. (e) . Mean Shannon-Wiener diversity. Note different axis scales.







Appendix 7.7 Mean values for diversity indices for individual biotopes within control and impact locations at each site. Samples are at family level, based on whole stones (U parts excluded). n = 3 samples.

INDEX SITE AND BIOTOPE	DEC		JAN		FEB		MAR		APR		MAY	
	Control	Impact	Control	Impact	Control	Impact	Control	Impact	Control	Impact	Control	Impact
S - total number of families or higher taxa												
Elands												
Riffle	11.7	17.7	12.3	10.7	12.3	11.0	12.7	8.3	9.3	17.3	8.0	13.3
Run	8.3	9.3	9.0	6.7	4.7	9.7	9.3	7.0	9.3	10.0	9.0	10.3
Pool	8.0	7.7	7.7	9.0	6.3	6.7	10.0	6.7	5.0	6.7	5.3	6.3
Molenaars												
Riffle	10.0	11.3	11.7	12.3	17.0	15.3	13.7	11.0	10.0	11.7	14.0	14.3
Run	10.3	11.0	10.0	11.7	12.3	8.7	10.0	11.0	13.0	12.3	9.3	10.0
Pool	6.0	10.0	7.3	6.0	7.0	7.0	11.0	7.0	9.0	6.0	5.0	7.0
Du Toits												
Riffle	15.0	19.0	9.0	12.3	14.7	7.3	9.3	10.7	11.3	11.3	17.0	13.3
Run	12.0	9.7	12.3	11.7	12.0	13.3	11.0	10.3	13.3	16.0	17.7	14.3
Pool	9.0	10.3	8.0	11.0	7.3	11.0	11.7	10.0	9.7	9.7	12.0	8.3
Riviersonderend												
Riffle	15.0	13.0	7.3	9.3	10.7	11.0	9.0	9.0	9.3	9.7	4.7	7.3
Run	7.7	9.7	5.0	8.7	5.7	6.7	9.7	9.0	6.3	7.3	7.3	8.3
Pool	9.0	7.7	7.3	6.0	8.3	6.0	5.7	5.7	7.7	4.3	7.3	5.0
N - total number of individuals												
Elands												
Riffle	1334.8	936.6	535.7	431.4	252.2	297.4	429.6	219.9	662.1	1275.3	212.1	349.2
Run	189.4	710.7	154.3	143.8	58.7	150.2	112.6	235.9	352.1	221.3	230.3	224.4
Pool	72.7	192.1	297.7	325.1	163.0	151.2	131.6	113.7	241.0	742.0	81.0	655.0
Molenaars												
Riffle	1900.9	1529.1	498.6	1466.2	1217.1	600.9	837.9	1070.0	2602.2	2744.8	1092.3	740.8
Run	1422.6	1204.9	443.6	438.3	210.3	215.9	310.7	446.4	1008.4	1275.0	351.8	396.0
Pool	484.1	143.7	258.1	61.5	144.1	131.2	164.0	110.5	218.6	111.9	204.8	220.7
Du Toits												
Riffle	1112.6	1131.0	811.0	1704.6	631.8	3876.2	3349.2	1101.7	2573.7	1427.4	944.7	753.9
Run	111.8	154.3	287.7	307.5	259.6	347.6	464.7	718.8	309.8	526.2	439.9	835.7
Pool	197.8	610.4	98.2	1541.4	177.8	224.1	203.6	147.5	200.0	246.7	151.2	136.2
Riviersonderend												
Riffle	409.9	324.5	204.9	376.5	552.8	791.8	510.8	273.2	233.8	121.5	93.7	195.2
Run	47.4	138.3	36.0	82.9	410.7	229.4	345.6	302.4	69.2	116.4	55.4	184.8
Pool	151.4	236.4	130.9	564.8	421.9	235.1	345.9	95.0	432.7	56.3	169.6	157.1
d - taxon richness												
Elands												
Riffle	1.484	2.480	1.835	1.613	2.098	1.901	1.938	1.347	1.353	2.290	1.363	2.131
Run	1.404	1.324	1.627	1.147	0.902	1.718	1.842	1.083	1.421	1.656	1.500	1.742
Pool	1.630	1.380	1.170	1.461	1.044	1.137	1.872	1.198	0.866	0.856	1.174	0.885
Molenaars												
Riffle	1.196	1.460	1.721	1.588	2.323	2.248	1.895	1.450	1.142	1.355	2.014	2.027
Run	1.297	1.453	1.474	1.760	2.132	1.440	1.552	1.656	1.763	1.622	1.420	1.512
Pool	0.918	1.803	1.237	1.219	1.300	1.221	1.988	1.293	1.483	1.042	0.760	1.132

Appendix 7.7 Continued.

INDEX SITE AND BIOTOPE	DEC		JAN		FEB		MAR		APR		MAY	
	Control	Impact	Control	Impact	Control	Impact	Control	Impact	Control	Impact	Control	Impact
***d* - taxon richness**												
Du Toits												
Riffle	1.994	2.575	1.299	1.539	2.122	0.875	1.098	1.406	1.341	1.493	2.339	1.917
Run	2.343	1.864	2.004	1.878	1.994	2.119	1.638	1.478	2.165	2.401	2.775	1.990
Pool	1.481	1.528	1.574	1.520	1.228	1.909	2.013	1.834	1.715	1.621	2.212	1.419
Riviersonderend												
Riffle	2.390	2.088	1.251	1.416	1.540	1.507	1.362	1.420	1.538	1.901	0.862	1.214
Run	1.735	1.831	1.347	1.953	0.792	1.057	1.517	1.423	1.273	1.386	1.665	1.440
Pool	1.627	1.225	1.303	0.798	1.212	0.946	0.812	1.065	1.119	0.860	1.280	0.794
***J'* - evenness**												
Elands												
Riffle	0.440	0.404	0.600	0.430	0.691	0.635	0.617	0.647	0.470	0.393	0.659	0.624
Run	0.442	0.305	0.467	0.541	0.805	0.688	0.707	0.630	0.516	0.689	0.677	0.665
Pool	0.615	0.578	0.387	0.605	0.606	0.666	0.660	0.448	0.608	0.404	0.720	0.407
Molenaars												
Riffle	0.437	0.355	0.456	0.359	0.558	0.649	0.600	0.646	0.393	0.485	0.536	0.438
Run	0.282	0.452	0.513	0.535	0.683	0.692	0.618	0.515	0.457	0.467	0.522	0.505
Pool	0.303	0.621	0.329	0.723	0.568	0.607	0.523	0.626	0.564	0.620	0.512	0.519
Du Toits												
Riffle	0.489	0.477	0.628	0.486	0.584	0.312	0.496	0.481	0.576	0.582	0.521	0.508
Run	0.724	0.746	0.638	0.668	0.539	0.814	0.699	0.547	0.659	0.568	0.586	0.436
Pool	0.744	0.618	0.877	0.598	0.741	0.738	0.857	0.807	0.838	0.769	0.704	0.477
Riviersonderend												
Riffle	0.509	0.493	0.621	0.552	0.580	0.510	0.575	0.502	0.606	0.630	0.726	0.638
Run	0.741	0.699	0.751	0.708	0.682	0.428	0.342	0.473	0.760	0.607	0.642	0.593
Pool	0.551	0.481	0.519	0.387	0.446	0.304	0.380	0.655	0.229	0.522	0.568	0.397
***H'* - Shannon-Wiener diversity**												
Elands												
Riffle	1.076	1.156	1.509	1.006	1.738	1.514	1.558	1.289	1.045	1.116	1.323	1.610
Run	0.937	0.651	1.024	1.012	1.231	1.457	1.553	1.124	1.153	1.496	1.475	1.507
Pool	1.270	1.165	0.801	1.185	1.088	1.268	1.529	0.790	0.960	0.717	1.148	0.765
Molenaars												
Riffle	0.975	0.866	1.124	0.898	1.567	1.753	1.560	1.538	0.906	1.183	1.360	1.159
Run	0.680	1.082	1.168	1.311	1.688	1.494	1.342	1.232	1.157	1.151	1.149	1.140
Pool	0.532	1.408	0.656	1.290	1.087	1.108	1.235	1.142	1.222	1.015	0.825	1.010
Du Toits												
Riffle	1.320	1.401	1.372	1.226	1.538	0.627	1.089	1.148	1.372	1.404	1.482	1.312
Run	1.761	1.663	1.563	1.640	1.340	2.076	1.581	1.287	1.685	1.575	1.679	1.163
Pool	1.432	1.441	1.754	1.412	1.469	1.745	2.104	1.829	1.803	1.742	1.729	1.185
Riviersonderend												
Riffle	1.298	1.262	1.222	1.215	1.374	1.222	1.252	1.107	1.312	1.417	1.125	1.259
Run	1.462	1.588	1.133	1.447	1.135	0.831	0.774	1.063	1.404	1.109	1.183	1.255
Pool	1.170	0.978	1.037	0.647	0.929	0.513	0.683	1.076	0.464	0.762	1.113	0.640

Appendix 7.8 Species of Chironomidae recorded at the sites. ● - present. ? - indefinite identification; nr - near; gen. nov. - new genus; sp. nov. - new species. Morpho species were indicated as sp. D, L, etc.

CHIRONOMIDAE	SPECIES	EL	MO	DU	RI
Chironominae					
Chironomini					
Cryptochironomus	spp.		●		
Harnischia[1]	?*curtilammellata*		●	●	
Microtendipes	*lamprogaster*			●	●
Polypedilum[2]	spp.	●	●	●	●
Stenochironomus	spp.	●			
Tanytarsini					
Cladotanytarsus[3]	spp.	●		●	●
Rheotanytarsus	*fuscus*	●	●	●	●
Stempellina	*truncata*		●	●	●
Tanytarsus	spp.	●	●	●	●
Afrozavrelia	*kribiensis*			●	●
Orthocladiinae					
Cardiocladius	*hessei*	●	●	●	
Corynoneura[4]	spp.	●	●	●	●
Corynoneura	*cristata*				●
Corynoneura[5]	sp. D		●		
Cricotopus[6]	spp.	●	●	●	●
Cricotopus	*kisantuensis*	●	●	●	●
Cricotopus[7]	sp. L			●	●
Cricotopus[8]	*dibalteatus*-type	●			
Cricotopus	sp. N				●
Cricotopus	sp. S	●			
Cricotopus	*obscurus*			●	●
Eukiefferiella	*clavigera*		●		●
Nanocladius[9]	spp.	●	●	●	●
Notocladius	*capicola*	●	●	●	●
Parakiefferiella	spp.				●
Parakiefferiella	*biloba*				●
Parakiefferiella	nr *ephippium*				●
Paradoxocladius[10]	*mangoldi*			●	●
Parametriocnemus	*scotti*				●
Paratrichocladius	*micans*				●
Pseudosmittia[11]	spp.			●	●
Rheocricotopus	*capensis*	●	●	●	●

Appendix 7.8 Continued.

CHIRONOMIDAE	SPECIES	EL	MO	DU	RI
Orthocladiinae cont.					
Thienemanniella	*lineola*	●	●	●	●
Thienemanniella	*trivittata*	●	●	●	●
Thienemanniella	sp. R	●	●	●	●
Thienemanniella[12]	sp. S		●		
Thienemanniella	sp. T		●		
Tvetenia	*calvescens*	●	●	●	●
Orthoclad[13]	sp. A	●	●	●	●
Tanypodinae[14]					
Ablabesmyia	*dusoleili*	●	●	●	●
Conchapelopia	*trifascia*	●	●	●	●
Larsia	spp.	●	●	●	●
Macropelopia[15]	*marmorata*			●	
Nilotanypus[16]	*comatus*	●	●	●	●
Paramerina	spp.	●	●	●	●

Notes:

[1] - *Harnischia* ?*curtilammellata* was only recorded from the substratum underlying stones for both sites (U sample parts).

[2] - Comprises the *Polypedilum* species *P. alticola* and *P. wittei*, with both present at all sites.

[3] - *Cladotanytarsus* spp. were recorded from only the substratum underlying stones at the DU site.

[4] - Comprises the two most common *Corynoneura* species, *C. elongata and C. dewulfi*.

[5] - *Corynoneura* sp. D was recorded from only the substratum underlying stones at the MO site.

[6] - Group of many species that are similar in the Western Cape with most larvae not associated with adults (includes: *C. flavozonatus, C. bergensis*, *C. obscurus*).

[7] - *Cricotopus* sp. L was recorded from only the substratum underlying stones at the DU site.

[8] - Possibly *C. dibalteatus.*

[9] - Majority of *Nanocladius* are *N. brunneus*, but *N. vitellinus* was occasionally recorded.

[10] - *Paradoxocladius mangoldi* gen. nov. (Harrison 2000), described as a new species during the study.

[11] - Comprises several species, of which *Pseudosmittia rectilobus* is most common. Recorded from only the substratum underlying stones at the DU site.

[12] - *Thienemanniella* sp. S was recorded from only the substratum underlying stones at the MO site.

[13] - Unknown orthoclad species (potential gen. nov.; Harrison pers. comm.) Recorded from only the substratum underlying stones at the MO site.

[14] - Tanypod juveniles (species indeterminate) were recorded from only the DU site, and were kept separate from other chironomids taxa during analysis.

[15] - *Macropelopia marmorata* was recorded from only the substratum underlying stones at the DU site.

[16] - Probably a species group.

Appendix 7.9 **Results of a SIMPER analysis comparing average abundances (0.1 m^{-2}) of chironomid species among site pairs.** $\overline{\delta}_i$ = the contribution of the *i*th species to the overall average dissimilarity ($\overline{\delta}$) between sites, expressed as a cumulative percentage ($\Sigma \overline{\delta}_i$ %). Data are derived from whole stones. Species are listed from greatest to least contribution to dissimilarity (cutoff at ≤ 50%), with the higher abundance for each species between groups indicated in bold.

$\overline{\delta}$ **BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL SPECIES**	**AVERAGE ABUNDANCE (0.1 m^{-2})**		$\overline{\delta}_i$	$\overline{\delta}_i$ / SD (δ_i)	$\overline{\delta}_i$ **%**	$\Sigma \overline{\delta}_i$ **%**
EL and MO = 33.64%	**EL**	**MO**				
Thienemanniella trivittata	16.53	**72.39**	3.24	1.35	9.64	9.64
Nilotanypus comatus	0.57	**4.91**	2.39	1.54	7.09	16.74
Cricotopus spp.	2.88	**16.08**	2.34	1.43	6.95	23.68
Notocladius capicola	16.75	**49.68**	2.24	1.22	6.66	30.35
Rheotanytarsus fuscus	4.71	**43.36**	2.12	1.12	6.31	36.65
Rheocricotopus capensis	0.37	**4.62**	1.99	1.47	5.90	42.55
Ablabesmyia dusoleili	0.09	**0.93**	1.85	1.72	5.50	48.06
Cricotopus kisantuensis	0.59	**0.90**	1.70	1.30	5.06	53.11
EL and DU = 39.29%	**EL**	**DU**				
Stempellina truncata	0.00	**13.70**	4.45	5.07	11.32	11.32
Notocladius capicola	16.75	**137.00**	3.42	1.39	8.70	20.01
Cricotopus spp.	2.88	**39.52**	3.24	1.95	8.25	28.26
Tanytarsus spp.	0.04	**3.65**	2.48	1.74	6.31	34.58
Rheocricotopus capensis	0.37	**8.47**	2.38	1.69	6.06	40.64
Thienemanniella trivittata	**16.53**	7.09	2.17	1.37	5.53	46.17
Tanypod juveniles	0.00	**2.23**	1.97	1.25	5.02	51.19
MO and RI = 48.64%	**MO**	**RI**				
Thienemanniella trivittata	**72.39**	0.38	3.86	1.68	7.94	7.94
Parakiefferiella biloba	0.00	**13.77**	3.39	3.09	6.97	14.91
Rheotanytarsus fuscus	**43.36**	1.16	2.79	1.52	5.73	20.64
Polypedilum spp.	1.77	**32.48**	2.60	1.97	5.35	25.98
Stempellina truncata	0.17	**5.78**	2.30	2.20	4.73	30.72
Orthoclad sp. A	0.00	**4.05**	2.30	2.21	4.73	35.44
Thienemanniella sp. R	0.27	**5.85**	2.20	1.51	4.52	39.96
Nilotanypus comatus	**4.91**	0.67	2.00	1.54	4.12	44.08
Thienemanniella lineola	3.92	**22.84**	1.58	1.22	3.25	47.33
Cricotopus sp. L	0.00	**4.87**	1.57	0.87	3.22	50.56

Appendix 7.9 Continued.

$\bar{\delta}$ BETWEEN SITES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL SPECIES	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\sum \bar{\delta}_i$ %
MO and DU = 33.99%	**MO**	**DU**				
Stempellina truncata	0.17	**13.70**	3.11	2.68	9.14	9.14
Thienemanniella trivittata	**72.39**	7.09	2.97	1.33	8.75	17.89
Notocladius capicola	49.68	**137.00**	2.53	1.44	7.44	25.33
Tanytarsus spp.	0.08	**3.65**	2.01	1.66	5.91	31.23
Nilotanypus comatus	**4.91**	0.24	1.95	1.81	5.74	36.97
Tanypod juveniles	0.00	**2.23**	1.71	1.25	5.05	42.02
Thienemanniella lineola	3.92	**19.74**	1.65	1.64	4.85	46.87
Rheotanytarsus fuscus	**43.36**	18.81	1.45	1.16	4.26	51.13
EL and RI = 50.65%	**EL**	**RI**				
Parakiefferiella biloba	0.00	**13.77**	3.88	3.07	7.67	7.67
Stempellina truncata	0.00	**5.78**	3.47	4.36	6.86	14.53
Thienemanniella sp. R	0.06	**5.85**	2.56	1.60	5.05	19.58
Thienemanniella trivittata	**16.53**	0.38	2.54	1.42	5.01	24.58
Orthoclad sp. A	0.02	**4.05**	2.50	2.04	4.94	29.53
Rheocricotopus capensis	0.37	**6.46**	2.27	2.06	4.49	34.02
Polypedilum spp.	3.43	**32.48**	2.17	1.90	4.28	38.30
Ablabesmyia dusoleili	0.09	**3.60**	2.09	1.54	4.12	42.42
Nanocladius spp.	0.13	**2.87**	1.84	1.30	3.64	46.06
Cricotopus sp. L	0.00	**4.87**	1.80	0.87	3.55	49.61
Tvetenia calvescens	**2.37**	1.54	1.72	1.27	3.39	53.01
DU and RI = 42.78%	**DU**	**RI**				
Parakiefferiella biloba	0.00	**13.77**	3.13	3.10	7.32	7.32
Notocladius capicola	**137.00**	35.61	2.28	1.46	5.34	12.66
Rheotanytarsus fuscus	**18.81**	1.16	2.11	1.49	4.93	17.58
Orthoclad sp. A	0.09	**4.05**	1.89	1.91	4.43	22.01
Thienemanniella trivittata	**7.09**	0.38	1.86	1.64	4.34	26.35
Thienemanniella sp. R	0.31	**5.85**	1.78	1.63	4.16	30.51
Conchapelopia trifascia	**6.65**	0.61	1.64	2.00	3.84	34.35
Tanytarsus spp.	**3.65**	0.24	1.60	1.46	3.73	38.08
Polypedilum spp.	5.06	**32.48**	1.55	1.59	3.62	41.70
Nanocladius spp.	0.03	**2.87**	1.54	1.26	3.61	45.31
Tanypod juveniles	**2.23**	0.00	1.53	1.24	3.57	48.88
Tvetenia calvescens	**3.18**	1.54	1.51	1.43	3.54	52.42

Appendix 7.10 Results of a SIMPER analysis comparing the chironomid assemblages of different biotopes at the Elands site. $\bar{\delta}_i$ = the contribution of the *i*th species to the overall average dissimilarity ($\bar{\delta}$) between biotopes, expressed as a cumulative percentage ($\Sigma \bar{\delta}_i$ %). Species are listed from greatest to least contribution to dissimilarity (cutoff at ≤ 50%), with the higher abundance for each species between groups indicated in bold.

$\bar{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL SPECIES	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma \bar{\delta}_i$ %
Riffle and Run = 47.45%	**Riffle**	**Run**				
Notocladius capicola	**46.95**	3.03	5.45	1.29	11.48	11.48
Rheotanytarsus fuscus	**12.14**	1.90	4.41	1.28	9.30	20.77
Thienemanniella trivittata	**30.79**	17.60	4.14	1.42	8.72	29.50
Tvetenia calvescens	**6.65**	0.40	3.74	1.17	7.88	37.38
Polypedilum spp.	**8.97**	1.06	3.63	1.14	7.66	45.04
Cricotopus spp.	**5.69**	2.82	3.31	1.11	6.97	52.00
Riffle and Pool = 74.89%	**Riffle**	**Pool**				
Notocladius capicola	**46.95**	0.28	8.93	2.22	11.92	11.92
Rheotanytarsus fuscus	**12.14**	0.09	7.91	3.23	10.57	22.49
Thienemanniella lineola	**17.32**	0.30	7.85	2.66	10.48	32.98
Thienemanniella trivittata	**30.79**	1.22	6.09	1.53	8.13	41.10
Polypedilum spp.	**8.97**	0.25	5.98	1.97	7.98	49.09
Cricotopus spp.	**5.69**	0.12	5.54	2.01	7.40	56.49
Run and Pool = 63.22%	**Run**	**Pool**				
Thienemanniella trivittata	**17.60**	1.22	8.45	1.38	13.37	13.37
Thienemanniella lineola	**5.05**	0.30	8.37	2.03	13.24	26.61
Paramerina spp.	0.08	**2.48**	6.96	1.32	11.01	37.62
Notocladius capicola	**3.03**	0.28	5.81	1.37	9.20	46.82
Cricotopus spp.	**2.82**	0.12	5.43	1.26	8.59	55.40

Appendix 7.11 Results of a SIMPER analysis comparing the chironomid assemblages of different biotopes at the Molenaars site.

$\bar{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL SPECIES	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma\bar{\delta}_i$ %
Riffle and Run = 37.17%	**Riffle**	**Run**				
Thienemanniella trivittata	80.10	**133.04**	4.19	1.37	11.28	11.28
Notocladius capicola	**124.12**	23.91	3.88	1.57	10.45	21.73
Rheotanytarsus fuscus	**90.76**	39.27	3.48	1.26	9.37	31.10
Rheocricotopus capensis	**9.56**	4.31	2.46	1.32	6.61	37.71
Cricotopus kisantuensis	**2.49**	0.21	2.29	1.40	6.17	43.88
Polypedilum spp.	2.10	**3.08**	2.28	1.66	6.14	50.02
Riffle and Pool = 72.59%	**Riffle**	**Pool**				
Rheotanytarsus fuscus	**90.76**	0.05	9.33	2.62	12.85	12.85
Notocladius capicola	**124.12**	0.99	8.83	2.14	12.16	25.01
Thienemanniella trivittata	**80.10**	4.04	6.72	1.47	9.25	34.26
Cricotopus spp.	**24.64**	1.30	5.53	1.94	7.62	41.87
Rheocricotopus capensis	**9.56**	0.00	4.60	1.50	6.34	48.22
Thienemanniella lineola	**5.77**	0.14	4.34	1.97	5.98	54.20
Run and Pool = 67.70%	**Run**	**Pool**				
Thienemanniella trivittata	**133.04**	4.04	9.27	1.41	13.70	13.70
Rheotanytarsus fuscus	**39.27**	0.05	7.32	1.57	10.81	24.50
Cricotopus spp.	**22.29**	1.30	5.74	1.52	8.49	32.99
Notocladius capicola	**23.91**	0.99	5.22	1.36	7.71	40.70
Conchapelopia trifascia	**2.93**	0.26	4.85	1.84	7.17	47.87
Tvetenia calvescens	**3.45**	0.00	4.76	2.07	7.03	54.89

Appendix 7.12 Results of a SIMPER analysis comparing the chironomid assemblages of different biotopes at the Du Toits site.

$\bar{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL SPECIES	AVERAGE ABUNDANCE (0.1 m^{-2})		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma\bar{\delta}_i$ %
Riffle and Run = 33.89%	**Riffle**	**Run**				
Notocladius capicola	**361.00**	49.29	4.39	1.43	12.95	12.95
Rheocricotopus capensis	**22.80**	2.10	2.96	1.54	8.74	21.69
Thienemanniella trivittata	8.62	**12.13**	2.57	1.31	7.57	29.26
Stempellina truncata	**20.03**	4.83	2.43	1.52	7.17	36.43
Rheotanytarsus fuscus	**44.26**	8.45	2.28	1.20	6.72	43.15
Tanytarsus spp.	**5.88**	4.77	2.12	1.18	6.27	49.42
Tvetenia calvescens	**7.68**	1.34	1.77	1.25	5.22	54.64
Riffle and Pool = 51.71%	**Riffle**	**Pool**				
Notocladius capicola	**361.00**	0.70	7.73	1.87	14.95	14.95
Rheocricotopus capensis	**22.80**	0.52	4.42	1.99	8.55	23.50
Rheotanytarsus fuscus	**44.26**	3.72	3.60	1.26	6.95	30.46
Thienemanniella lineola	**39.62**	1.86	3.34	1.84	6.47	36.92
Tvetenia calvescens	**7.68**	0.53	3.02	1.77	5.83	42.76
Thienemanniella trivittata	**8.62**	0.52	2.89	1.44	5.59	48.35
Stempellina truncata	**20.03**	16.25	2.84	1.30	5.50	53.85
Run and Pool = 45.70%	**Run**	**Pool**				
Notocladius capicola	**49.29**	0.70	4.52	1.69	9.88	9.88
Tanypod juveniles	0.00	**6.68**	3.32	1.25	7.26	17.15
Thienemanniella trivittata	**12.13**	0.52	3.21	1.13	7.02	24.16
Stempellina truncata	4.83	**16.25**	2.89	1.24	6.32	30.48
Rheotanytarsus fuscus	**8.45**	3.72	2.75	1.11	6.03	36.51
Cricotopus spp.	**57.42**	13.13	2.75	1.40	6.02	42.53
Paramerina spp.	1.30	**6.05**	2.74	1.39	5.99	48.52
Tanytarsus spp.	**4.77**	0.31	2.65	1.20	5.80	54.32

Appendix 7.13 Results of a SIMPER analysis comparing the chironomid assemblages of different biotopes at the Riviersonderend site.

$\bar{\delta}$ BETWEEN BIOTOPES AND RELATIVE CONTRIBUTIONS BY INDIVIDUAL SPECIES	AVERAGE ABUNDANCE ($0.1\ m^{-2}$)		$\bar{\delta}_i$	$\bar{\delta}_i$ / SD (δ_i)	$\bar{\delta}_i$ %	$\Sigma\bar{\delta}_i$ %
Riffle and Run = 45.33%	**Riffle**	**Run**				
Notocladius capicola	**95.22**	10.29	3.77	1.55	8.32	8.32
Parakiefferiella biloba	4.66	**18.81**	2.96	1.34	6.53	14.85
Orthoclad sp. A	**9.44**	2.33	2.74	1.52	6.05	20.90
Cricotopus spp.	**29.41**	6.88	2.47	1.40	5.44	26.35
Thienemanniella sp. R	1.98	**14.09**	2.28	1.37	5.04	31.39
Conchapelopia trifascia	**1.65**	0.00	2.23	1.60	4.92	36.30
Thienemanniella lineola	12.80	**38.27**	2.23	1.18	4.91	41.21
Cricotopus sp. L	4.25	**9.04**	2.15	0.78	4.75	45.97
Rheocricotopus capensis	**12.02**	4.50	2.10	1.29	4.64	50.60
Riffle and Pool = 54.41%	**Riffle**	**Pool**				
Notocladius capicola	**95.22**	1.32	5.55	1.97	10.20	10.20
Cricotopus spp.	**29.41**	3.27	3.55	1.38	6.53	16.73
Orthoclad sp. A	**9.44**	0.39	3.09	1.67	5.68	22.40
Ablabesmyia dusoleili	0.22	**9.43**	2.92	1.51	5.36	27.76
Parakiefferiella biloba	4.66	**17.84**	2.82	1.27	5.18	32.94
Rheocricotopus capensis	**12.02**	2.87	2.66	1.35	4.88	37.82
Polypedilum spp.	14.12	**79.40**	2.61	1.53	4.80	42.62
Nanocladius spp.	0.42	**6.96**	2.32	1.24	4.26	46.88
Thienemanniella sp. R	**1.98**	1.49	2.07	1.41	3.80	50.68
Run and Pool = 51.45%	**Run**	**Pool**				
Polypedilum spp.	3.91	**79.40**	3.82	1.72	7.42	7.42
Thienemanniella sp. R	**14.09**	1.49	3.35	1.40	6.50	13.93
Parakiefferiella biloba	**18.81**	17.84	3.11	1.06	6.04	19.96
Thienemanniella lineola	**38.27**	17.44	3.10	1.30	6.02	25.98
Ablabesmyia dusoleili	1.16	**9.43**	3.08	1.34	6.00	31.98
Cricotopus spp.	**6.88**	3.27	2.80	1.24	5.44	37.42
Notocladius capicola	**10.29**	1.32	2.80	1.32	5.44	42.86
Nanocladius spp.	1.24	**6.96**	2.61	1.18	5.07	47.93
Rheocricotopus capensis	**4.50**	2.87	2.35	1.37	4.56	52.49

Appendix 8.1 Tolerance ranges for select hydraulic habitat variables, for potential indicator families at natural low flows. Families showing both highly significant biotope specificity and correlations with one or more hydraulic variables were selected.

FAMILY	*N*	DEPTH				MEAN COLUMN VELOCITY				NEAR-BED VELOCITY				FROUDE NUMBER			
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Acarina	222	0.121	0.088	0.004	0.690	0.295	0.295	0	1.423	0.272	0.283	0	1.423	0.329	0.355	0	1.855
Elmidae	231	0.122	0.083	0.004	0.500	0.280	0.294	0	1.423	0.259	0.280	0	1.423	0.313	0.349	0	1.855
Hydraenidae	39	0.108	0.064	0.020	0.250	0.405	0.329	0	1.408	0.391	0.322	0	1.408	0.458	0.397	0	1.589
Chironomidae	318	0.128	0.098	0.004	0.770	0.237	0.275	0	1.423	0.216	0.261	0	1.423	0.260	0.327	0	1.855
Empididae	23	0.133	0.108	0.020	0.500	0.499	0.312	0	1.273	0.461	0.310	0	1.170	0.516	0.345	0	1.336
Athericidae	98	0.126	0.084	0.020	0.500	0.323	0.272	0	1.289	0.297	0.256	0	1.170	0.353	0.326	0	1.524
Simuliidae	191	0.120	0.092	0.004	0.690	0.342	0.297	0	1.423	0.316	0.286	0	1.423	0.381	0.360	0	1.855
Baetidae	316	0.128	0.099	0.004	0.770	0.239	0.275	0	1.423	0.218	0.261	0	1.423	0.262	0.327	0	1.855
Caenidae	33	0.125	0.101	0.004	0.420	0.132	0.236	0	1.067	0.095	0.206	0	1.067	0.119	0.277	0	1.524
Teloganodidae	246	0.130	0.101	0.004	0.770	0.223	0.271	0	1.423	0.201	0.256	0	1.423	0.237	0.312	0	1.855
Corixidae	25	0.109	0.085	0.005	0.420	0.121	0.252	0	1.110	0.114	0.236	0	0.971	0.127	0.268	0	1.121
Notonectidae	11	0.091	0.054	0.005	0.180	0.029	0.080	0	0.267	0.024	0.068	0	0.227	0.027	0.077	0	0.257
Pyraustidae	22	0.092	0.058	0.030	0.240	0.500	0.455	0	1.408	0.462	0.431	0	1.408	0.559	0.474	0	1.589
Oligochaeta	152	0.122	0.083	0.020	0.500	0.338	0.303	0	1.423	0.310	0.292	0	1.423	0.376	0.378	0	1.855
Hydropsychidae	95	0.099	0.066	0.020	0.300	0.433	0.296	0	1.423	0.409	0.285	0	1.423	0.514	0.367	0	1.855
Hydroptilidae	122	0.126	0.099	0.004	0.690	0.336	0.290	0	1.334	0.308	0.274	0	1.319	0.363	0.334	0	1.524
Leptoceridae	168	0.125	0.097	0.004	0.690	0.181	0.229	0	1.273	0.162	0.215	0	1.170	0.191	0.263	0	1.524
Philopotamidae	47	0.105	0.075	0.004	0.280	0.442	0.359	0	1.423	0.399	0.346	0	1.423	0.524	0.444	0	1.855

Appendix 8.2 Tolerance ranges for select hydraulic habitat variables, for potential indicator chironomid species at natural low flows. Species showing both highly significant biotope specificity and correlations with one or more hydraulic variables were selected.

SPECIES	*N*	DEPTH				MEAN COLUMN VELOCITY				NEAR-BED VELOCITY				FROUDE NUMBER			
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Rheotanytarsus fuscus	100	0.101	0.070	0.004	0.340	0.347	0.289	0	1.423	0.322	0.278	0	1.423	0.411	0.372	0	1.855
Cricotopus spp.	127	0.108	0.076	0.004	0.420	0.325	0.293	0	1.423	0.297	0.280	0	1.423	0.378	0.371	0	1.855
Cricotopus kisantuensis	11	0.080	0.063	0.020	0.250	0.541	0.207	0.121	0.856	0.492	0.214	0.121	0.829	0.711	0.336	0.146	1.145
Notocladius capicola	129	0.117	0.093	0.004	0.690	0.332	0.288	0	1.423	0.305	0.278	0	1.423	0.385	0.371	0	1.855
Rheocricotopus capensis	71	0.102	0.069	0.020	0.360	0.382	0.300	0	1.423	0.356	0.299	0	1.423	0.467	0.409	0	1.855
Thienemanniella lineola	131	0.113	0.086	0.004	0.690	0.329	0.291	0	1.423	0.302	0.281	0	1.423	0.388	0.373	0	1.855
Tvetenia calvescens	52	0.105	0.075	0.020	0.360	0.413	0.295	0.001	1.423	0.390	0.292	0.001	1.423	0.492	0.407	0	1.855
Ablabesmyia dusoleili	29	0.126	0.084	0.005	0.340	0.043	0.123	0	0.558	0.032	0.092	0	0.326	0.043	0.116	0	0.428
Conchapelopia trifascia	63	0.113	0.074	0.020	0.430	0.339	0.271	0	1.289	0.309	0.260	0	1.081	0.379	0.331	0	1.524
Paramerina spp.	46	0.114	0.078	0.005	0.420	0.111	0.199	0	0.869	0.106	0.204	0	0.829	0.124	0.230	0	0.925

PLATES

Plate 3.1 **Biophysical character of the Elands site, with the control location in the foreground and a run patch delimited.**

Plate 3.2 **Elands impact location, with pool and riffle biotopes shown.**

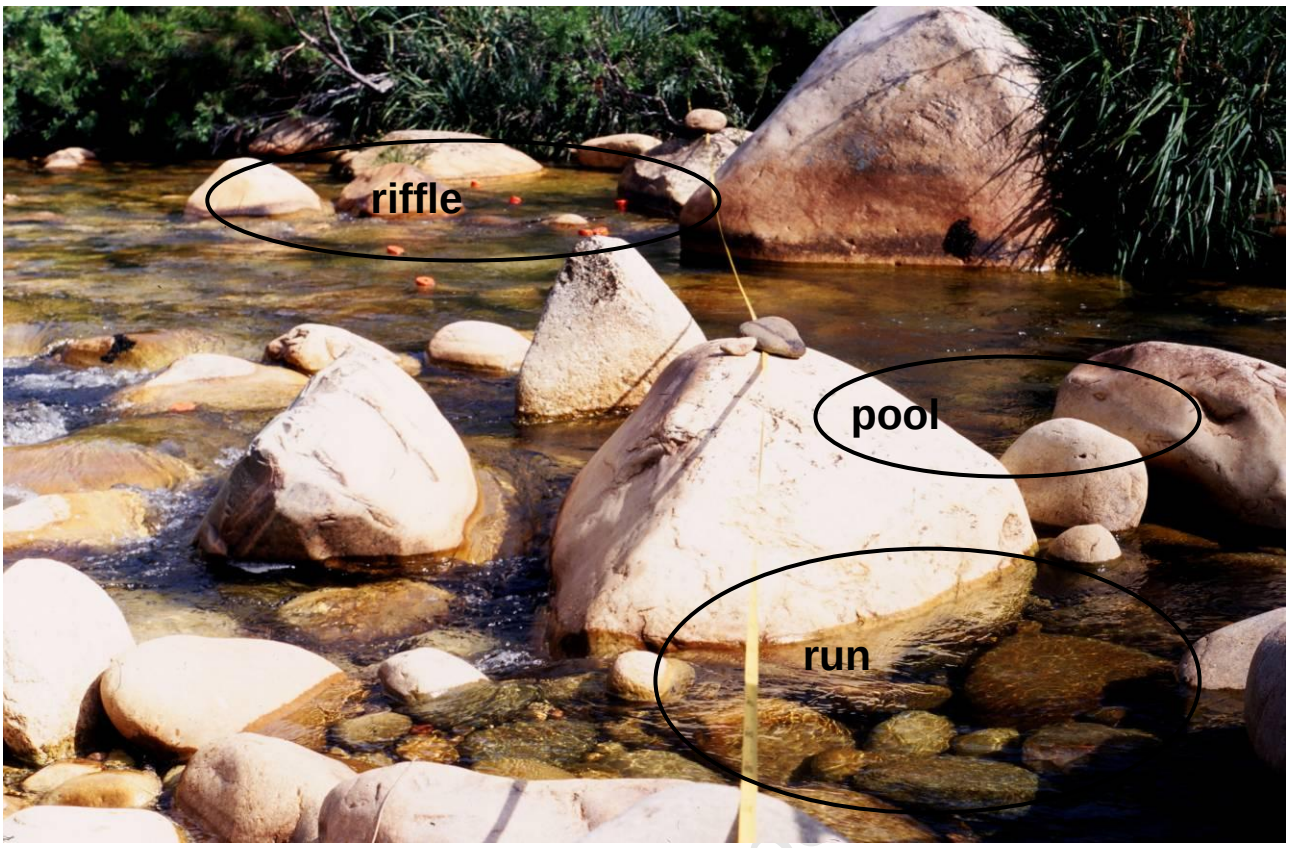


Plate 3.3 **Control location of the Molenaars site, showing riffle, run and pool biotopes and microhabitat sample points (orange markers).**

Plate 3.4 **Upper section of the Molenaars impact location, downstream of the DWAF gauging weir, with the offtake pipes for temporary flow diversion towards the left bank.**

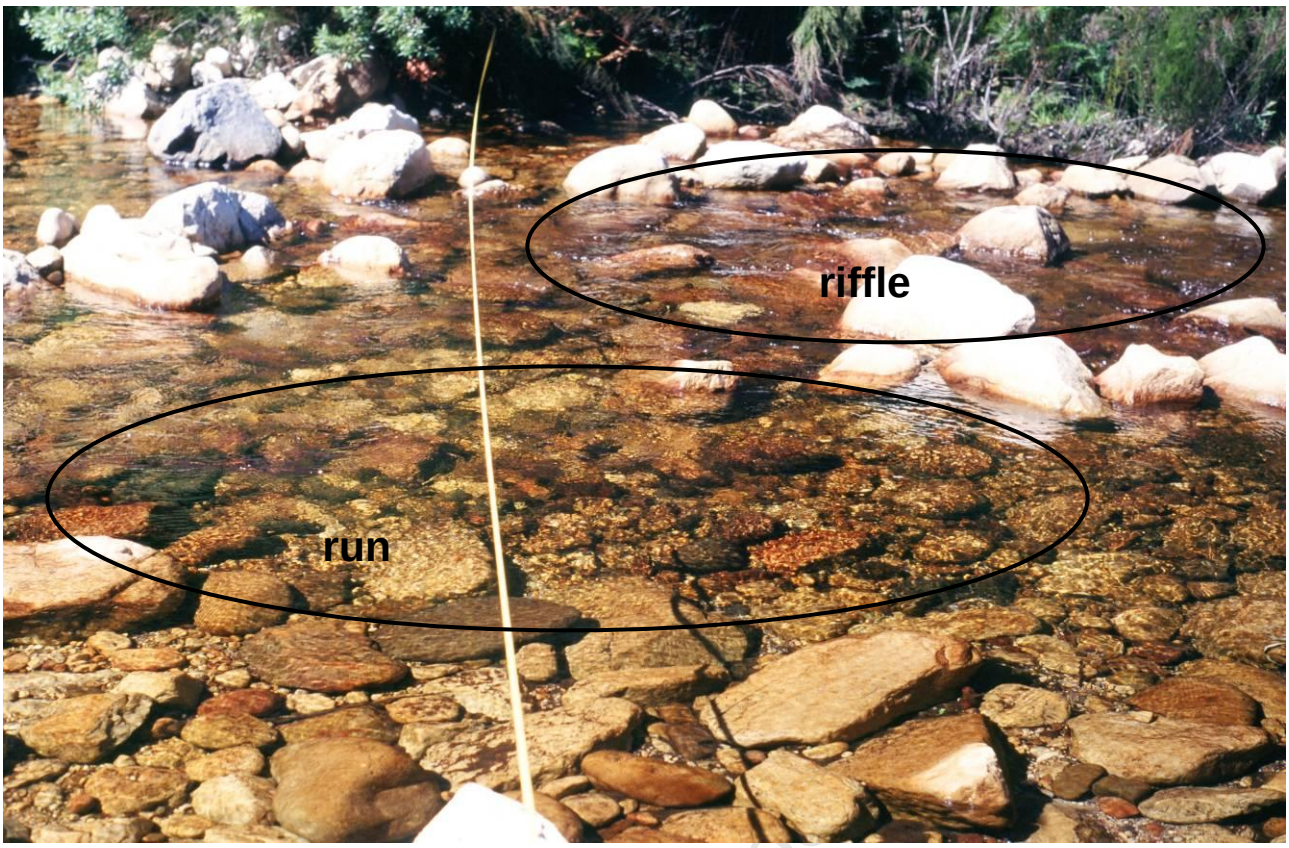


Plate 3.5 **Control location of the Du Toits site, with a survey tape indicating the approximate location of the run cross-section.** Run and pool biotopes are demarcated.

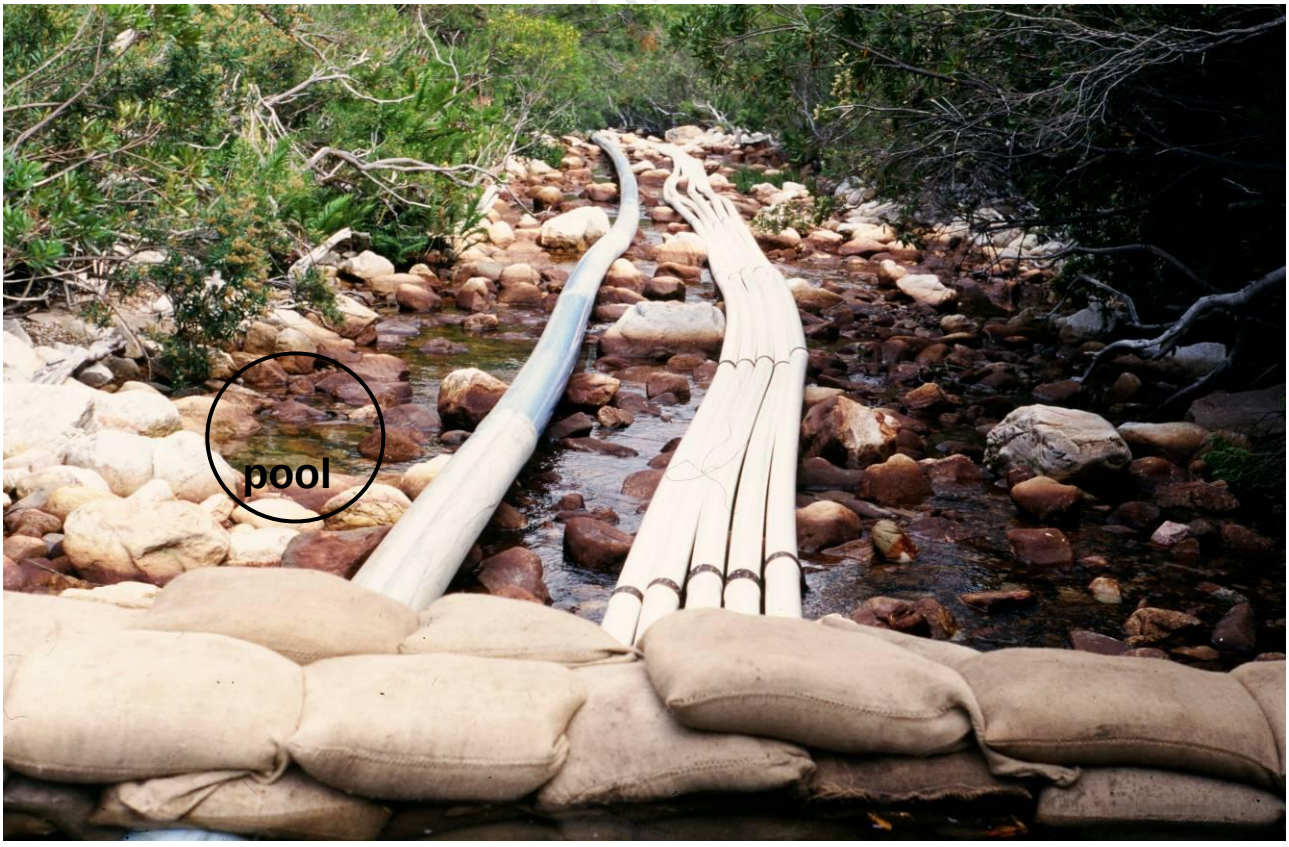


Plate 3.6 **Du Toits impact location with the temporary diversion weir immediately upstream, in the foreground, and a marginal pool delineated.**

Plate 3.7 **Control location of the Riviersonderend site, with a riffle patch delineated.**

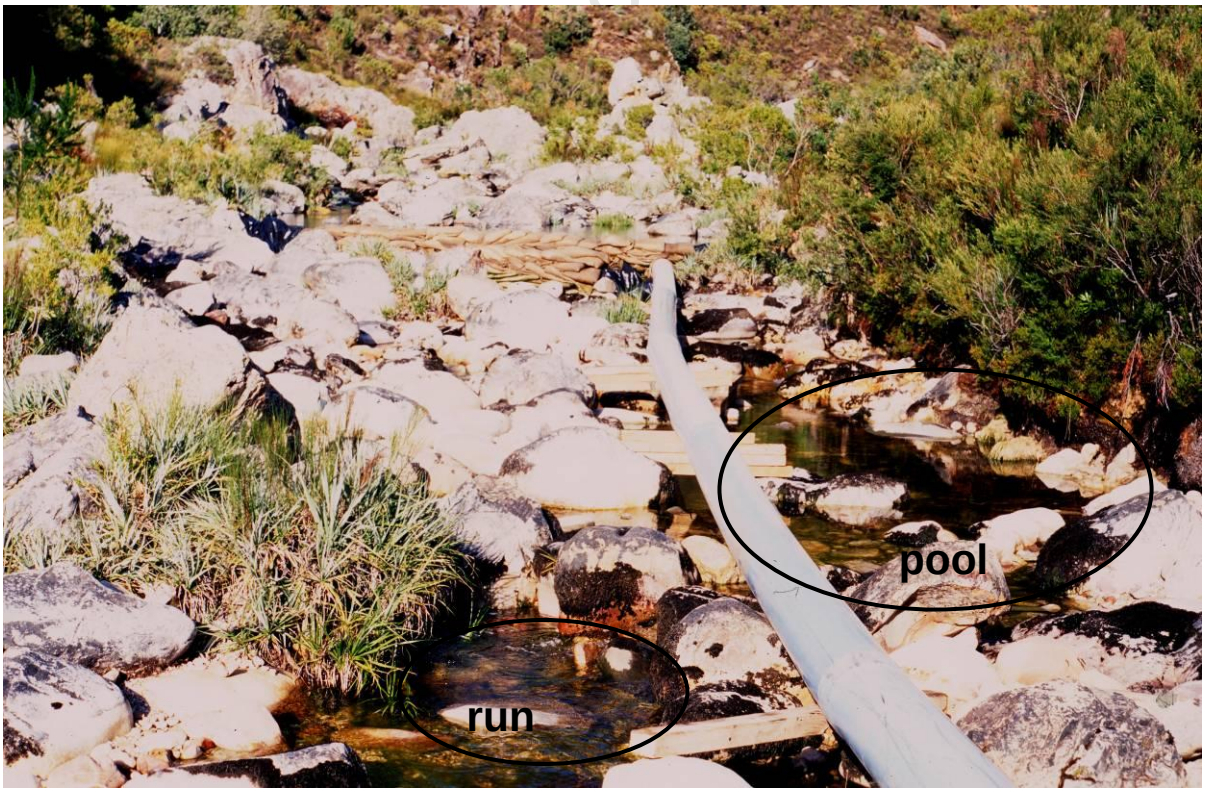


Plate 3.8 **Riviersonderend impact location, showing temporary diversion weir and pipe propped on boulders/wood blocks.** Pool with massive algal growth and run demarcated.

Plate 3.9 **First stage of construction of the temporary diversion weir for the Riviersonderend site.**

Plate 3.10 **Patch of previously fully submerged substratum, near a diversion pipe, exposed and desiccated due to extreme flow reduction in the Du Toits impact location.** Natural water level apparent on the top left.

Plate 3.11 **Exposed boulders with partially desiccated *Isolepis digitata* and proliferating filamentous green algae, due to extreme low flows in the Riviersonderend impact location.**

Plate 3.12 **A pool in the Riviersonderend impact location, entirely isolated from areas of flowing water due to extreme flow reduction, with partially exposed small boulders and aquatic vegetation.** It exhibited elevated conductivity and discoloured water.